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BREEDING BEHAVIOR AT SUCCESSIVE GENERATIONS FOLLOWING HYBRIDIZATION IN SOYBEANS

by

Robert Rankin Kalton

A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject: Crop Breeding

Approved:

Signature was redacted for privacy.

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INTRODUCTION

Extensive breeding investigations with soybeans in this country have been underway for only a relatively short period of time. Breeding work was at first confined primarily to introduction and selection, but it was soon realized that the possibilities for continued improvement with these practices were definitely limited. Consequently, during the last ten or fifteen years, hybridization has rapidly supplanted these procedures as the principal means for obtaining new and improved varieties.

Methods of handling segregating populations of crosses in such self-pollinated crops as wheat, oats, barley, and flax now are fairly well standardized. Practices involve various modifications of the pedigree method, the bulk method, or a combination of the two. An advantage of the pedigree method is that it enables the investigator to conduct inheritance studies of characteristics in which the parents differ. The principal advantages of the bulk method are cheapness in cost and opportunity to conduct replicated bulk yield tests as early as the F_2 generation. Early generation yield testing with the pedigree method, on the other hand, is limited or practically impossible in certain crops because of the scarcity of seed produced on individual plants and the high cost of testing large numbers of lines in replicated tests. Segregating populations of soybean crosses are admirably adapted for breeding by either of the two methods. In addition, comparatively large seed yields on spaced individual plants makes it possible to conduct pedigree yield tests as early as the F_3 generation. It is feasible, therefore, to use replicated tests for the evaluation of agronomic potentialities of soybean crosses in the early segregating generations following hybridization with either the bulk or the pedigree method of breeding.

Available evidence from replicated tests of F_2 and F_3 populations of wheat and barley crosses indicates that this procedure may be of value in estimating the yield potentialities of such crosses. Similar evidence of the merits of early generation testing for yield and other agronomic characters in soybean crosses is not available, as yet, in any substantiating amounts. There is a need, therefore, for experimental data on such practices as they pertain to the handling of segregating populations of crosses in this crop. The investigations reported herein were conducted in an attempt to obtain additional information relative to this problem.

In this study the agronomic performance of several different soybean crosses was measured at the first four generations following hybridization. Both the bulk and the pedigree methods were used in these evaluations. It was thought, by so doing, that at least partial answers might be obtained to some of the questions concerned with the potentialities of early generation testing in soybean crosses. A few of the more salient of these questions are listed as follows:

1. Are measurements made on spaced F_1 plants in different crosses of any value in predicting the agronomic performance of subsequent segregates?

2. Are differences in the mean agronomic performance of bulk populations of crosses, as shown

by replicated trials in the F_2 generation, substantiated by similar bulk tests in the F_3 and F_4 generations in the following years?

3. Is there any correlation between the agronomic characteristics of individual F_2 and F_3 plants and their progeny means in succeeding generations?

4. To what extent is segregation for factors conditioning yield, maturity, height, and lodging resistance among F_2 and F_3 plants in different crosses indicated by replicated tests of their progenies in the next generation?

5. Are there sufficient differences among F_4 progenies to warrant selection for yield in the parental F_3 lines?

6. How do the bulk and the pedigree methods of handling segregating populations of soybean crosses compare with each other in the evaluation of agronomic differences in early generations following hybridization?

The potential value of early testing in soybean crosses depends to no small extent on the nature of the answers to these and related questions. Consequently, they are given consideration wherever possible in the presentation and discussion of the results obtained in these experiments.

REVIEW OF PERTINENT LITERATURE

Hayes and Immer (10) classify as naturally self-pollinated those crops which generally show less than 4.0% cross-pollination. Soybeans were included in this group. Actual experimental evidence indicates that the amount of natural crossing in this crop is considerably less than 4.0%. Piper and Morse (23) found, in a bulk lot of seed, several off-colored seeds whose plants produced progenies that segregated in a Mendelian fashion for pubescence and seed coat colors. They postulated that the amount of natural crossing was quite small - possibly .50%. In the same report, the authors reported results of bagging and caging a number of individual plants. These plants set seed as well as non-bagged and non-caged plants, thereby indicating complete self-fertility. In an experiment specifically designed to test the amount of natural crossing, Woodworth (34) found .16% natural crossing. Similar studies by Garber and Odland (4) showed .14% natural crossing one year and .36% the next. These results all indicate that soybeans are better than 99.0% self-fertilized under natural conditions.

Hybridization has been used in the improvement of self-pollinated crops for a number of years. Several breeding methods utilizing hybridization have been employed successfully by the breeders of the self-pollinated cereals. Two of these are the pedigree method and the bulk method. The essential feature of the pedigree method is that successive generations following hybridization are grown under such conditions that the ancestry of each individual is known. This involves making individual plant selections each year starting with the F_2 generation and continuing in this manner until each progeny row is homozygous enough for bulking. Each year during this period selections are generally made first on a row basis and then on a plant basis. The straight bulk method consists of growing the populations of each cross in bulk starting with the F_2 generation and continuing as such until the F_6 or F_7 generation. At that time, the component plants of each population are usually homozygous enough for selection and subsequent testing in progeny rows. An outline of a general order of procedure for employing each of these methods is given by Hayes and Immer (10) and Love (19). Harrington (8) has proposed a combination of these two methods into what he calls the "mass-pedigree method". It consists of growing the segregating populations in bulk starting with the F_2 generation and making plant selections whenever environmental conditions provide suitable differentials for selection. As an example, he suggested selecting for lodging resistance or disease resistance in any year that these conditions are extreme. In a subsequent year, the pedigree method is followed.

Examples of the successful use of the pedigree method of breeding following hybridization in small grains are very numerous. A number of such examples are illustrated in Hayes and Immer (10). Illustrations of the successful use of the bulk method, however, are not as frequent or as widely publicized. The main reason for this probably lies in the fact that the pedigree method has been used much more commonly than the bulk method in this country. Florell (3) employed the bulk method with a number of wheat crosses in California with good results. In that study nineteen wheat crosses were carried in bulk to the F_5 and F_6 generations. Desirable head selections were made at that time and grown in progeny rows the succeeding year. The forty-five best progeny rows were selected and the seed from each bulked and used to plant a replicated yield test. Thirty-three of the forty-five selections (73.3%) outyielded the standard variety included as a check in the test. The selections also showed good lodging and shattering resistance.

The growing of bulk populations of a mixture of several crosses is a modification of the bulk method that has been used by several breeders of self-pollinated cereals. If large enough bulked lots are grown each year, it is assumed that this modification will allow for extensive segregation and recombination of factors conditioning the desired characteristics. It is also believed that many of the weak undesired types in the bulk populations are eliminated by natural selection when this procedure is used. Adair and Jones (1) grew three such mixtures of rice crosses in one location each in Texas, Arkansas, and California for eight years, starting with the F_3 generation. In the ninth year, a sample of seed from each of the nine bulk lots was grown at Stuttgart, Arkansas and studied for the survival of desirable genotypes. Although the proportions of different types varied in the lots from different locations, all bulk lots contained enough desirable agronomic types for satisfactory selection purposes. Harlan and Martini (5) reported the pending initiation of a large composite mixture of barley crosses. Equal quantities of seed from the F_2 generations of all possible crosses between twenty-eight varieties of barley were to be included in this composite. The parent varieties for these crosses were selected to represent all the major barley producing areas of the world. Each variety exhibited one or more features which merited its use in crosses. After growing this composite hybrid mixture for five years, it was hoped that segregation, recombination, and natural selection would enable the isolation of a number of new, homozygous desirable types.

Harlan, Martini and Stevens (6) grew 379 barley crosses for seven generations in separate rows to maintain the identity of each cross. Each year a bulk sample of seed of each cross was planted in a single, ten foot nursery row and the yields taken. On the basis of the average yields of each cross during this period, single plant selections were made in a space-planted plot of each cross in the eighth generation. More selections were taken from the higher yielding than from the lower yielding bulk crosses. In all, 2,921 plant selections were made at that time. Simultaneously, another 2,921 of the most desirable plants were selected in a space-planted plot of the composite hybrid mixture described in the previous paragraph. These 5,842 selections were tested in non-replicated rows in the next generation with appropriate check varieties. It was found that the average yields of the bulk crosses during the preselection period were soundly indicative of the yield performance of the selections made therefrom and tested in the ninth generation. The selections made from the composite mixture of crosses, however, were as high in average yield as the selections made from the pedigree crosses. These results were considered as justifying the elimination of lower yielding crosses on the basis of their non-replicated yield performance during the segregating generations before selection is practiced.

The potentialities of yield testing bulk populations of crosses in the early generations following hybridization have been studied by several other small grain breeders. Harrington (9) tested bulk populations of six wheat crosses in replicated trials during the F_2 and F_3 generations and found considerable differences in yield among the six crosses. Replicated yield tests of lines selected from these crosses in the F_6 to F_8 generations substantiated their early generation yield performance. He did not believe, however, that such tests could be used to evaluate crosses for such characters as milling and baking quality, disease resistance, etc. in the early segregating generations. Immer (14) compared the bulk populations of six barley crosses in replicated trials in the F_2, F_3, and F_4 generations. Some crosses were consistently higher in yield than others in these tests. The average performance of the same crosses in a space-planted test in the F_1 generation did not agree with the yield performance of the bulk crosses in drilled plots in the succeeding generations. It was suggested that such tests might be used to eliminate poorer yielding crosses in the early generations following hybridization since they would contain fewer high yielding genotypes than higher yielding crosses.

An evaluation of the characteristics of a number of F_2 plants is another method that has been suggested as a possible means for predicting the potentialities of any given cross. In the wheat cross, Marquillo x Marquis, Harrington (7) grew an F_2 population of nearly 40,000 plants. Only six lines of questionable value were retained from this cross after five years of rigid pedigree selection for desired characters. Originally, the cross promised a combination of the best features of the two parents. An analysis of a random sample of several hundred F_2 plants from this cross gave a similar prediction as to the very limited possibilities for obtaining the desired recombinations. Characters which were successfully predicted by the F_2 analysis were: rust resistance, plant height, maturity, and seed appearance. The average seed yield of all F_2 plants in comparison with the average parental plant yields, however, did not correctly predict the yield performance of the subsequently selected lines. Immer (15) measured the means and variances of the seed yields of four F_2 crosses and four varieties of barley in a replicated space-planted test. The mean yields of the varieties and the mean yields of the F_2 crosses were both significantly different among themselves. The variance of seed yields per plant within plots, however, was not much greater for the F_2 crosses than it was for the comparable parent varieties. Consequently, it was concluded that the variation in seed yields of single plants in space-planted progeny rows was determined almost completely by environmental factors.

The use of early generation testing has not been limited to the evaluation of segregating populations of crosses in the self-pollinated cereals. Its use in cotton breeding has been advocated and studied by several investigators. Hutchinson (12) suggested the use of modern statistical designs to subject breeding material to rigorous tests any time beyond the single plant stage. By this process one could determine for each character the earliest possible generation at which efficient selection and critical comparisons might be made. In a replicated, space-planted study of the parents and F_1 and F_2 generations of three intraspecific crosses in cotton, Hutchinson, Panse, and Govande (13) found that the environment was responsible for the greatest proportion of the total variance of agronomic characters among F_2 plants. They concluded that single plant selection for staple length, ginning percentage, and certain other characters in progeny rows in the F_2 generation was likely to be inefficient. This study was continued by Panse (21) who grew replicated progenies of a sample of the F_2 plants in each cross in the F_3 generation and studied them for staple length. The regression coefficients of the mean staple length of the F_3 progenies on the F_2 plants were highly significant in two of the three crosses. He considered it advantageous, therefore, to select individuals whose staple length exceeded the mean plot value in the replicated test of spaced F_2 plants.

Early testing of inbred lines of corn is, in a way, comparable to early generation testing of crosses in self-pollinated crops. The two methods are similar in that they are both used in an attempt to estimate the genotypic value of subsequent segregates. Available information on the relative merits of early testing of inbred lines of corn is somewhat contradictory. Probably the first experimental evidence directly favoring early testing of inbred lines of corn was obtained by Jenkins (16). He measured the effect of inbreeding upon the hybrids made after successive generations of selfing and found that the lines apparently acquired their individuality as top cross parents relatively early in the inbreeding process. Thereafter, the lines tended to retain such individuality. These results suggested the possibility for evaluation of inbred lines for combining ability as early as the S_1 or S_2 generation. In another study, utilizing top cross performance as a measure of combining ability, Jenkins (17) found only a limited segregation for factors conditioning yield prepotency among individual plants within seven S_1 lines. These results were considered as further justification for early testing of inbred lines of corn. Sprague (26) also obtained some substantiating evidence in favor of early testing of corn inbreds. He grew a top cross test of 167 S_0 plants from a stiff-stalk synthetic. S_1 plants representing the high 10.0% of this S_0 top cross yield distribution were tested in a similar manner and their S_1 top cross yields were found equivalent to the yields of the selected parents. In a later test, three S_3 lines from this selected group gave a better average yield performance in single crosses than several standard commercial inbreds.

Sprague and Bryan (27) studied the segregation of genes conditioning yield prepotency, lodging, and disease resistance in F_3 and F_4 lines of corn and obtained evidence of significant segregation for these factors in both generations. In the top cross tests of the F_4 lines, however, the F_3 families showed considerably greater variation for these characters than their F_4 progenies. Conflicting evidence pertaining to the early testing of corn inbreds was obtained by Singleton and Nelson (24) who evaluated the combining ability of successive generations of inbred sweet corn. They did not find any correlation between combining ability in the S_0, S_1, or S_2 generations and the S_3 generation in the lines studied. In addition they were able to increase combining ability (for yield) from the S_0 to the S_3 generation by intensive selection.

In a discussion of the theoretical aspects of small grain breeding Leighty (18) emphasized the need of knowledge of genetic principles for the development of sound breeding practices with any crop. Mode of pollination, hybridization potentialities, linkage relationships between characters, and adaptation to the environment were a few of the things which he stressed. Such principles apply to soybean as well as to small grain breeding. In fact, much of the earlier breeding work with soybeans was directed along these very lines. Many of the first soybean crosses were made principally to study the inheritance of certain plant and seed characters. The results of these studies showed that a number of characters were inherited in a simple Mendelian fashion. A few linkage groups also were established as a consequence of these experiments. Summaries of this early genetic work with soybeans were made by Woodworth (36) and Morse and Cartter (20).

Another phase of the earlier breeding work with soybeans were studies relating to the factors contributing to yield of seed. Woodworth (36) listed some of these factors as: number of nodes per plant, number of pods per node, number of seeds per pod, percentage of abortive seed, and seed weight. He stated that a knowledge of such yield attributes would enable crosses to be made so that the opportunities for desirable combinations in the resulting segregates would be enhanced. Woodworth (37) compared replicated spaced plants of a number of soybean varieties and found the varieties to differ widely, on the average, for the various yield components and for seed yield itself. Only two of the components, however, were significantly correlated with yield. They were percentage of abortive seed which was negatively correlated and seed weight which was positively correlated with yield. Weatherspoon and Wentz (31) made a detailed study of the relationships between certain plant characters and seed yield in 237 strains of soybeans. Of the characters measured, number of pods per plant, number of pods per node, number of nodes per plant, and plant height each were highly significantly correlated with seed yield per plant in a positive manner. Seed size and percentage of abortive seed were not related to yield to any appreciable extent. Partial regression coefficients for yield on these characters showed that the two main factors contributing to yield were plant height and number of pods per plant. Number of nodes per plant was associated with yield primarily because of its association with plant height. In a study of F_2 plant populations of several soybean crosses Stewart (28) obtained higher correlations between plant height and yield in crosses between bushy types than in crosses between viny types. He also measured a number of individual plants in a pure line of soybeans and found the number of pods per plant, number of nodes per plant, number of branches per plant, and plant height all highly correlated with seed yield per plant.

Other investigators have shown time of maturity to influence soybean seed yields to a considerable extent, depending on environmental conditions. Davis (2) grew a replicated test of thirty-seven pure line selections from a single soybean cross and obtained a highly significant positive correlation between date of maturity and yield among the selections in both years that the test was conducted. Weiss, Weber, and Kalton (32) found the relationship between maturity and yield to vary considerably with the type of season. In a year with early frost yield was negatively correlated with time of maturity. In late frost years, however, yield was positively associated with maturity. These studies were conducted with a number of F_2 plants, F_3 lines, and F_4 lines of seventeen crosses grown in successive years.

The nature and extent of heterosis in the F_1 and later generations of soybean crosses has been evaluated by numerous workers. Wentz and Stewart (33) measured the heights and seed yields of a few F_1 and parental plants in each of several soybean crosses and found some evidence of hybrid vigor for plant height. Only one of the crosses, however, exceeded both parents in plant height. Their data on seed yield per plant showed striking indications of hybrid vigor for this character in F_1 plants.

Woodworth (37) compared several F_1 plants of two soybean crosses with the parents. Both of the F_1 crosses exceeded the higher parent in average number of branches per plant, average number of nodes per plant, average plant height, and average number of pods per plant. One of the F_1 crosses exceeded both parents in average seed yield per plant, while the other was intermediate between the two parents for the same character.

Veatch (29) also demonstrated the existence of heterosis in the F_1 generation of soybean crosses. He went a step further, however, and studied the F_2 plant populations of several crosses in comparison with their parents. In this comparison he obtained evidence that indicated transgressive segregation for seed yield, seed number, height, and number of days from planting to flowering among the F_2 plants in each cross. None of these F_2 populations averaged significantly above the higher yielding parent in seed yield per plant and all averaged between the parents in plant height. Except for a few cases, the F_2 populations in each cross were somewhat more variable than plants of the parental varieties for the characters studied. Similar evidence on the extent of heterosis and variability for certain agronomic characters shown in the F_2 generation of different soybean crosses was obtained by Stewart (28). The most extensive information pertaining to hybrid vigor in soybean crosses has been presented by Weiss, Weber, and Kalton (32). In a replicated plant test (under greenhouse conditions) of seventeen F_1 crosses and their parents they obtained higher average seed yields per plant than either parent in sixteen of the seventeen F_1 crosses. The other F_1 cross was lower in average yield than the mean of the two parents. In a field test of the same crosses the average seed yields per plant of from twenty-eight to sixty-five competitive F_1 and parental plants grown in adjacent rows were compared. In this test all F_1 crosses exceeded the higher yielding parent in average seed yield per plant. The extent of heterosis for seed yield per plant among the different F_1 crosses varied considerably, however, between the greenhouse and the field. Average date of plant maturity, average plant height, and average lodging resistance per plant of the F_1 crosses were consistently between that of the parents in all crosses included in the test.

The adaptability of soybean crosses to early generation testing procedures, as used in small grain breeding work, depends to a considerable extent on the breeding behavior for desired characters at successive generations following hybridization. Despite the large number of segregating populations of soybean crosses that have been grown in recent years, there is little experimental evidence pertaining to this subject. Patel (22), in an attempt to determine if high yielding F_3 plants had high yielding progenies, grew duplicate progeny rows of 249 F_3 plants in the F_4 generation and measured them for seed yield. Three different soybean crosses were represented in this study. He found a definite tendency for the high yielding F_3 plants to have high yielding progeny rows in the next generation. Henson (11) bulked the seed from each of the twenty-five highest yielding F_4 rows in each of these three crosses and used it to plant a replicated yield test in the F_5 generation. The mean seed yields of the seventy-five strains differed considerably among themselves. Moreover, he found that the average yields of the selections in the F_5 generation were definitely related to the yields of their parental F_4 rows the previous year. One of the best of these bulk F_5 strains was continued in bulk until the F_7 generation, at which time it was grown in a space-planted plot. Weatherspoon (30) selected 237 plants in this plot, measured them for seed yield, and used the seed to plant a five foot progeny row of each the next year. These progeny rows were measured for seed yield and their seed in turn used to plant a replicated yield test of all strains in the next generation. The correlations for seed yield among these three successive generations of the 237 lines were as follows:

F_7 plant and F_8 progeny row, $r = .0162$
F_7 plant and F_9 mean yield, $r = .1282$
F_8 progeny row and F_9 mean yield, $r = -.003$

This decided lack of association was considered as indicating the uselessness of selecting for yield on a single plant or single progeny row basis.

The results of the replicated test of these 237 strains in the F_9 generation were analyzed by Weatherspoon and Wentz (31). The analyses of variance showed that the strain means differed significantly for plant height, number of nodes per plant, number of pods per node, number of seeds per pod, percentage of abortive seed, seed size, and seed yield. The mean differences were highly significant for all characters except percentage of abortive seed, whose differences were only significant. As these strains all originated from the same F_3 plant, the results indicated little homozygosity in the F_3 generation for factors conditioning the characters included in the study. Thirty-seven of the highest yielding F_9 lines were selected for further testing in replicated trials by Davis (2). These yield tests were grown in 1933 and repeated again in 1935. He found significant differences in mean yield among the strains in both years. The rank in yield of the strains, however, was somewhat different for each year, as indicated by a significant strain x year interaction. The yields in this test were not evaluated as to their relationship with results of previous generations.

Weiss, Weber, and Kalton (32) used both the bulk and the pedigree methods of breeding to test the agronomic performance of seventeen soybean crosses during the early segregating generations. They found that the degree of heterosis for seed yield, as determined on spaced F_1 plants, was of little or no value in estimating the yield potentialities of subsequent segregates from a cross. Average plant measurements for seed yield and date of maturity based on replicated, spaced F_2 plant populations, on the other hand, were indicative of cross differences in later generations in respect to these characters. Bulk populations of each of these crosses, including the bulk F_2 through the bulk F_5 generations, were grown together in one replicated test. In this test the mean seed yield, maturity date, lodging score, and plant height of each population were determined. As significant interactions were obtained between generations and crosses in the analysis of variance for each character, no one bulk generation sufficed to accurately evaluate the relative differences in agronomic performance among the crosses. The average height and degree of lodging resistance of the bulk populations were useful in predicting the performance of subsequent selections for these characters. This was not true to any appreciable extent for average seed yield and date of maturity. In the pedigree phase of the study they found that maturity readings on spaced F_2 plants were highly correlated with the mean maturities of their progenies in the F_3 generation. Similar associations for yield were of a considerably lesser magnitude. Replicated tests of F_3 and F_4 lines, each of which descended from single F_2 and F_3 plants, respectively, resulted in good estimates of future expectations for maturity, height, and lodging resistance. Replicated pedigree-progeny tests for seed yield in the early segregating generations, however, were noticeably influenced by seasonal differences in the environment. As a result, evaluation for this character did not appear justified before possibly the F_4 generation.

MATERIALS AND METHODS

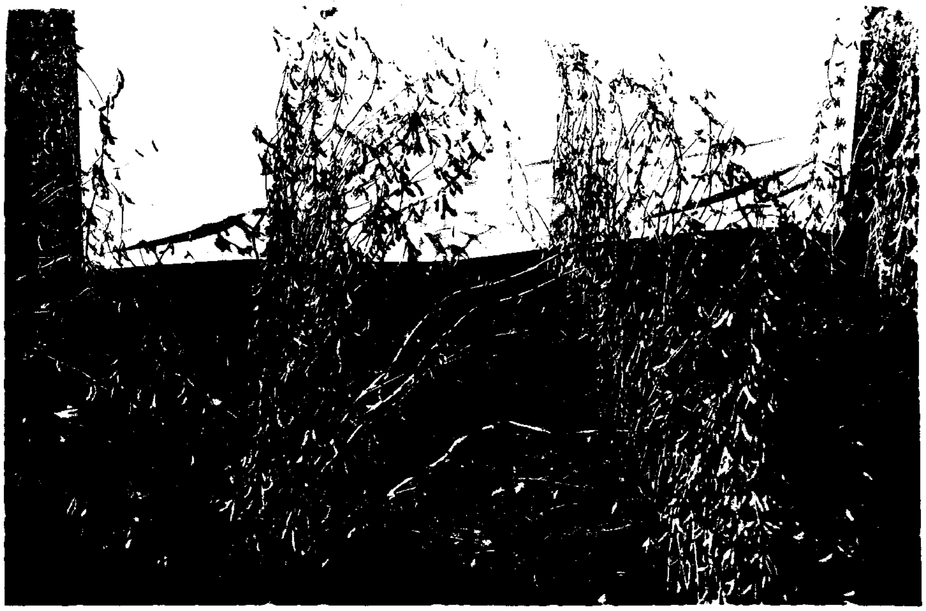
During the period from 1936 to 1940 a large number of soybean varieties and plant introductions were tested at various locations in Iowa. Many of these strains were discarded on the basis of their poor performance in these tests. A few, although not significantly better in performance than the varieties in commercial production, were sufficiently promising in one or more features to merit their use as parents in a hybridization program. Since most of those selected as parental material for crosses were lacking in lodging resistance, they all were crossed to the Richland variety. Richland was selected as the common parent because of its outstanding lodging resistance, good seed yield, satisfactory oil content of the seed, and relatively early maturity. In all, twenty-five of these crosses were made in the summer of 1941. The F_1 through the F_4 generations of these crosses constituted the material studied in this investigation.

The F_1 generation of these crosses was grown in 1942. In each cross the F_1 plants were planted between the two parents in rows spaced thirty-two inches apart. Within the rows the plants of the parents and the F_1 generations were uniformly spaced one foot apart. By this method of planting it was possible to compare the average seed yields per plant of the F_1 generation with either parent and the mean of the two parents. However, since only four of the crosses were selected for intensive study, only the F_1 results with these are presented in comparison with the parents.

The same four crosses were remade in 1945 and tested again in 1946. These crosses were as follows: Mukden x Richland, Manchuria 13-177 x Richland, P. I. 79885 x Richland, and P. I. 89009-2 x Richland. A comparison of each of the other four parents with Richland is shown in Figures 1 to 4.

In the cross, Mukden x Richland, in 1942, only adjacent competitive plants of the parents and F_1 generation were measured for seed yield. In the other three crosses all available plants of each were harvested for yield determinations, irrespective of competition. Data on agronomic characters other than yield were not taken in 1942. In 1946, however, maturity and height were evaluated in addition to yield. The manner of planting was changed in 1946 so that plants of both parents and the F_1 generation were alternately spaced in each row. Plants within the row were spaced eight inches apart. This method resulted in a total separation of only sixteen inches between the three plants in each paired comparison. Although this method reduced the number of competitive comparisons, it increased the accuracy of the results by decreasing the amount of soil heterogeneity. The F_1 generations were evaluated for average seed yield and height per plant as a percentage of either parent or the mean of the two parents. Maturity was expressed as the number of days earlier (-) or later (+) than either parent or the mean of the two parents.

The seed harvested from all of the F_1 plants in each of the twenty-five crosses was composited in the winter of 1942-1943. This bulked seed was used to plant a bulk population yield test of the F_2 generation in 1943. In addition to the bulk crosses, Lincoln and Richland



Mukden Richland

Fig. 1. Parents of the cross, Mukden x Richland (Cross No. 1415).

Richland Manchuria 13-177

Fig. 2. Parents of the cross, Manchuria 13-177 x Richland (Cross No. 2715).

Richland P.I. 79885

Fig. 3. Parents of the cross, P.I. 79885 x Richland (Cross No. 3515)

Richland P.I. 89009-2

Fig. 4. Parents of the cross, P.I. 89009-2 x Richland (Cross No. 3715).

were entered twice and Mukden once as check varieties to give a total of thirty entries in a randomized complete block design with six replications. Each replication of an entry consisted of a single, drilled eighteen foot row which was trimmed to sixteen feet just before harvest. Another portion of the bulked seed of each cross was planted in a separate plot for generation advancement. Using the same procedures, yield tests of the bulk F_3 and the bulk F_4 generations were grown in 1944 and 1945, respectively. A small test of the bulk F_3 generation of only the four crosses selected for special study was grown in 1945. In this test Lincoln, Richland, and Mukden each were entered once as check varieties in a randomized complete block design with six replications. The rows were spaced thirty-two inches apart in the 1943 and 1944 tests and three feet apart in the 1945 tests.

Measurements were taken on the following agronomic characters of each cross in the bulk F_2, F_3, and F_4 tests: yield of seed, maturity, height, and lodging susceptibility. The consistency in expression of these characters by the bulk populations of the twenty-five crosses at successive generations in consecutive years was evaluated by the use of correlation coefficients. These correlations were calculated between the F_2 and F_3 generations, the F_2 and F_4 generations, and the F_3 and F_4 generations for each agronomic character.

On the merits of their performance in the bulk F_2 and F_3 yield tests in 1943 and 1944, respectively, the two highest and two of the lowest yielding bulk crosses were selected for investigation on a pedigree basis.

The two highest yielding bulk crosses were, namely, Mukden x Richland and Manchuria 13-177 x Richland. The two low yielding bulk crosses were P. I. 79885 x Richland and P. I. 89009-2 x Richland. They already have been discussed in previous paragraphs.

Since the bulk F_3 data were not yet available in the spring of 1944, a space-planted plot of the F_2 generation of twenty of the crosses was planted that year. The seed used for this planting was remnant seed of the composited lots harvested from the F_1 plants of each cross in 1942. A random sample of 200 of these seeds from each cross was planted in a thirty-two inch row with a uniform spacing of eight inches between plants within the row. Similar plots of Lincoln, Richland, and Mukden also were included. In the fall of 1944, the first 100, consecutive competitive plants in each cross were tagged. Individual plant measurements were made on these plants for seed yield, maturity, and plant height. Frequency distributions, means, standard deviations, and coefficients of variation were calculated for each character using the data gathered from the plants in each cross and variety. These data provided estimations of the amount of variability for each character in the F_2 generation of the crosses as compared to the parental varieties. However, since the research was continued into the F_3 and F_4 generations on a pedigree basis with only four of the crosses, only the F_2 plant data from these four and the plant data from the three varieties are presented as experimental results for this phase of the investigation.

The study of these four crosses on a pedigree basis at successive generations was continued in the F_3 generation in 1945. During that season a pedigree yield test of the progenies of most of the F_2 plants in each cross was grown. The first seventy-seven of the 100 F_2 plants which produced sufficient seed for planting the F_3 test were selected to represent each F_2 population. In addition, the two parents and the bulk F_2 and F_3 generations of each cross were included, giving a total of eighty-one entries per cross. The planting plan for each cross consisted of three replications of a 9 x 9 triple lattice. Each entry in a replication consisted of a single, drilled eight foot row with each row spaced three feet apart. This test, hereafter called the F_3 line test, was designed so that not only the differences between lines within crosses but also the differences between crosses could be ascertained. To do this, the first replication, group X, of each cross was randomized on a cross basis. The same was done with replication 2, group Y, and replication 3, group Z. Measurements were taken on seed yields, maturities, heights, and lodging susceptibilities of the F_3 lines in the fall of 1945. Analyses of variance for each of the characters were calculated subsequent to harvest. The relationships between the F_2 plants grown in 1944 and the means of their progenies in the F_3 line test in 1945 were determined for each character by the use of correlations.

A space-planted row of each of the seventy-seven F_3 lines per cross was grown in a separate nursery in 1945. In the fall of that year, the first five plants in each row were harvested and threshed individually.

Their seed was used to plant the F_4 line test in 1946. Because it was impossible to test the progenies of all F_3 lines, it was necessary to take a representative sample of the F_3 lines in each cross for continuing the study into the F_4 generation. This was done by first eliminating the extremely early and late F_3 lines in each cross, thereby minimizing a possible bias from positive correlations between maturity and yield. In this manner the number of F_3 lines in each cross was arbitrarily reduced to sixty. They were then ranked according to yield from highest to lowest. As fifteen lines appeared about the maximum that could be progeny tested in each cross, the yield arrays were separated into fifteen groups of four each. Using a random start from one to four for each cross, every fourth line thereafter was selected to make up the total of fifteen lines per cross. Each F_3 line thus selected was represented in the F_4 test in 1946 by the progeny of five F_3 plants.

In all, seventy-five F_4 lines (five F_4 lines for each of fifteen F_3 lines) from each cross were grown in a randomized split plot design in 1946. Also included in the test were the parents and bulk F_3, F_4, and F_5 generations, thus making a total of eighty entries per cross. The design was such that three sets of differences for each agronomic character under investigation could be measured. These differences were those between crosses, between F_3 family progenies, and between the five F_4 lines representing each F_3 family. Each F_4 line in the test was replicated three times with each replication consisting of a single, drilled eight foot row spaced three feet apart. Each replication of the four crosses was randomized first on a cross basis, then on an F_3 family progeny basis for each cross, and finally on an F_4 line basis. This planting procedure resulted in the greatest accuracy for evaluating the differences between the F_4 lines of any F_3 family. Measurements were taken on the same agronomic characters in the F_4 line test in the fall of 1946 as were taken in the F_3 line test in 1945. The relationships between the F_2 plants in 1944 and the means of their five descendant F_4 lines in 1946 were evaluated for each agronomic character by the use of correlations. For the cross, Mukden x Richland, the availability of F_3 single plant data enabled the calculation of a further correlation between F_3 plants and their F_4 line means.

A frequent subject for discussion among soybean breeders is whether or not a relationship exists among maturity, height, lodging susceptibility, and yield in segregating populations of soybean crosses. In order that some further information pertaining to this question might be obtained, the simple and partial correlations between certain of these characters were calculated from the data obtained in the pedigree tests of the F_2, F_3, and F_4 generations in 1944, 1945, and 1946, respectively. Of the possible correlations, only those within each year were determined.

All the tests in this investigation were conducted at the Agronomy Farm, Ames, Iowa. The methods used for evaluating each of the agronomic characters studied were as follows:

<u>Seed yield</u> - all seed was dried to a uniform moisture before weighing. Plant seed yields were determined

in grams. Plot yields were adjusted to a bushels per acre basis.

Maturity - plants or plots were considered mature when 90 to 100% of the pods had turned brown and most of the leaves had fallen. Maturity was taken as the calendar date or the number of days after September 1 when this stage was reached.

Height - plants or plots were measured in inches for average height from the ground to the highest point on the mature plants.

Lodging - plots were assigned lodging scores which ranged from a score of 1, where most plants in the row were perfectly erect, to a score of 5, where most plants were prostrate.

Statistical and experimental procedures, as outlined in Snedecor (25) and Hayes and Immer (10), were used throughout the course of these experiments.

EXPERIMENTAL RESULTS

F_1 Generation Spaced Plant Study

Assuming a judicious choice of parents, the first opportunity to measure the potentialities of any cross occurs in the F_1 generation. In a highly cross pollinated crop such as corn, the performance of the hybrid is of primary importance and usually easy to determine. In self-pollinated crops, on the other hand, the performance of the F_1 generation is not only difficult to determine but also of questionable significance. The number of crossed seeds that can be obtained in such self-pollinated crops as wheat, oats, barley, and soybeans is very limited in most breeding programs. This limitation decidedly impairs the accuracy of agronomic measurements made in the F_1 generation. Moreover, even if accurate F_1 information could be obtained, it might not necessarily be indicative of the consequences of segregation and recombination that result from continued self-pollination in subsequent generations. Experimental evidence on the latter point is not in abundance, as most investigators have not related the performance of the F_1 generation with that of segregates from the same cross in advanced generations. It is questionable, therefore, whether or not any of the agronomic potentialities of a cross can be ascertained through appropriate tests in the F_1 generation of self-pollinated crops. In this study an attempt was made to obtain information on the F_1 generation of several soybean crosses and to relate this information to the breeding behavior in subsequent generations.

Yield

Although it is especially difficult to obtain large numbers of crossed seeds in soybeans, enough were produced to make limited comparisons of certain agronomic characteristics in the F_1 generation with those of the two parents. Measurements of seed yields were made in both 1942 and 1946 on a single plant basis. The mean seed yields in grams per plant for the F_1 generations of four soybean crosses as compared to those of the parents appear in Table 1. The 1942 results with the cross, Mukden x Richland, are the most reliable because only adjacent competitive plants of the F_1 generation and the parents were used for determining yields. This cross also had the greatest number of plants. In the other three crosses in 1942, all plants of the F_1 generation and the parents in each cross were harvested from adjacent rows without respect to competition. However, the number of competitive and non-competitive plants was approximately the same for the two parents and the hybrid so that the comparisons seemed worthy of inclusion. Only competitive plants were evaluated in each cross in 1946. Plants of each of the parents and the F_1 generation for each cross were alternately planted eight inches apart in the same row, as previously described.

The average seed yield per plant for the F_1 generation of each cross was expressed as a percentage of each parent and the mean of the two parents in Table 1. The F_1 plants of all crosses produced a higher average seed yield per plant than the mean of the two parents

Table 1. Mean seed yields in grams per plant for the F_1 generations of four soybean crosses as compared to the yields of the parents.

Parent or hybrid	Number of plants	Grams of seed per plant	Mean seed yield of parents	F_1 in percentage of: P_1	P_2	Mean of parents
		1942 Results				
Mukden	42	67.7				
Mukden x Richland	42	71.9	64.8	106.2	116.2	111.0
Richland	42	61.9				
Manchuria 13-177	20	56.5				
Manchuria 13-177 x Richland	21	80.6	52.3	142.7	167.6	154.1
Richland	21	48.1				
P.I. 79885	13	67.7				
P.I. 79885 x Richland	12	89.6	64.4	132.3	146.4	139.1
Richland	13	61.2				
P.I. 89009-2	27	52.0				
P.I. 89009-2 x Richland	25	67.2	48.3	129.2	150.7	139.1
Richland	28	44.6				
		1946 Results				
Mukden	5	49.2				
Mukden x Richland	5	43.0	41.5	87.4	127.2	103.6
Richland	5	33.8				
Manchuria 13-177	2	69.0				
Manchuria 13-177 x Richland	2	60.0	54.3	87.0	151.9	110.5
Richland	2	39.5				
P.I. 79885	4	39.8				
P.I. 79885 x Richland	4	58.3	43.4	146.5	124.0	134.3
Richland	4	47.0				

Table 1 (Continued)

Parent or hybrid	Number of plants	Grams of seed per plant	Mean seed yield of parents	F_1 in percentage of: P_1	P_2	Mean of parents
P.I. 89009-2	5	54.0				
P.I. 89009-2 x Richland	5	55.0	44.6	101.9	156.3	123.3
Richland	5	35.2				

in both years. It should be noted, however, that the amount of superiority varied considerably from cross to cross. In 1942, the F_1 generation of all crosses exceeded the higher yielding parent, while in 1946 this occurred with only two of the four crosses. Since Richland was a common parent to each of the crosses, comparisons of the F_1 plant yields with it are of interest. The F_1 crosses, Manchuria 13-177 x Richland and P. I. 89009-2 x Richland, exceeded the Richland parent to the greatest extent in yield in both years. The F_1 cross, Mukden x Richland, produced the smallest average increase in yield over the Richland parent of the four crosses in 1942 and was second lowest in 1946. If F_1 yields were related to the potentiality of obtaining high yielding segregates in later generations, the expectation would be that the cross, Mukden x Richland, would be the least promising of the four crosses from a yield standpoint.

Maturity

Time of maturity is another agronomic character which is generally considered of importance in soybean crosses. The mean maturities for the F_1 generations of the four soybean crosses as compared to the maturities of the parents in 1946 are presented in Table 2. The average maturity of the F_1 plants was intermediate

Table 2. Mean maturities in number of days after September 1 for the F_1 generations of four soybean crosses as compared to the maturities of the parents.

Parent or hybrid	Number of plants	Mean maturity	Mean maturity of parents	F_1 expressed as days earlier (-) or later (+) than: P_1	P_2	Mean of parents
Mukden	5	33.6				
Mukden x Richland	5	32.2	31.1	-1.4	+3.6	+1.1
Richland	5	28.6				
Manchuria 13-177	2	48.5				
Manchuria 13-177 x Richland	2	39.0	40.0	-9.5	+7.5	-1.0
Richland	2	31.5				
P.I. 79885	5	30.6				
P.I. 79885 x Richland	5	31.2	30.2	+ .6	+1.4	+1.0
Richland	5	29.8				
P.I. 89009-2	4	37.0				
P.I. 89009-2 x Richland	4	38.5	34.6	+1.5	+6.2	+3.9
Richland	4	32.3				

between the two parents in two of the crosses and slightly later than either parent in the other two. It seemed possible, therefore, that the potentialities of securing segregates later than either parent in subsequent generations were greater with the crosses, P.I. 89009-2 x Richland and P.I. 79885 x Richland, than with the other two crosses. As will be shown, this supposition proved to be true for the latter cross in the advanced generations.

Plant height

Comparative measurements on plant height were obtained in 1946 on a few parental and F_1 plants in each cross. These mean height measurements are shown in Table 3. In only one of the four crosses, namely, P. I. 89009-2 x Richland, were the F_1 plants taller on the average than either parent. In the other three crosses the F_1 plants were intermediate between the two parents. In light of these results it might have been expected that the possibilities of finding segregates taller than either parent were greatest in the cross, P.I. 89009-2 x Richland, and less in the other crosses. Likewise, the opportunity for finding segregates exceeding Richland in height in the cross, P.I. 79885 x Richland, seemed somewhat remote. As will be seen in later sections, these predictions actually were correct. However, it also will be shown that these observations made in the F_1 generation were not necessarily indicative of the extensiveness of segregation for plant height in later generations.

Table 3. Mean heights in inches for the F_1 generations of four soybean crosses as compared to the heights of the parents.

Parent or hybrid	Number of plants	Mean height	Mean height of parents	F_1 in percentage of: P_1	P_2	Mean of parents
Mukden	5	45.4				
Mukden x Richland	5	41.4	40.2	91.2	118.3	103.0
Richland	5	35.0				
Manchuria 13-177	2	47.0				
Manchuria 13-177 x Richland	2	42.5	41.8	90.4	116.4	101.7
Richland	2	36.5				
P.I. 79885	5	26.6				
P.I. 79885 x Richland	5	29.8	30.4	112.0	87.1	98.0
Richland	5	34.2				
P.I. 89009-2	5	26.6				
P.I. 89009-2 x Richland	5	36.6	30.4	137.6	107.0	120.4
Richland	5	34.2				

Bulk Population Tests

The simplest method of testing bulk crosses in a practical breeding program with self-pollinated crops is to grow successive generations in consecutive years. This procedure eliminates the necessity of maintaining seed stocks in storage for several years or the remaking and continued growing of successive generations so that several bulk generations can be tested in the same year. It also removes the possible undesirable consequences of differential seed viability resulting from storage. With a crop like soybeans, however, this method has certain definite disadvantages. Soybeans are quite sensitive to damage from early frosts, especially when full-season adapted varieties are grown. Relative differences among varieties are known to vary considerably with seasonal and locality fluctuations in the environment. Furthermore, in the early segregating generations the proportions of early and late segregates in bulk populations of crosses may be altered by the time of occurrence of the first killing frost in the fall each year. Consequently, these factors provide limitations to the breeding value of early generation testing of bulk crosses in soybeans, even though this procedure might actually be indicative of the potentialities of future segregates when testing is carried out under uniform conditions.

Yield

In this study the bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses were tested in successive years with three of the commercially important parental varieties included as checks. Table 4 shows the average seed yields and yield ranks of the crosses and the

Table 4. Mean seed yields in bushels per acre and yield ranks of bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses and three check varieties grown in successive years.

Cross or variety	Cross number	Bulk F_2 1943 (Bu.)	Rank	Bulk F_3 1944 (Bu.)	Rank	Bulk F_4 1945 (Bu.)	Rank	Average 1943 to 1945 (Bu.)	Rank
Dunfield x Richland	1115	46.3	4	37.2	5	34.9	17	39.5	4
Illini x Richland	1315	45.2	8	35.8	15	33.3	23	38.1	18
Mukden x Richland	1415	48.1	1	37.1	7	37.0	2	40.7	1
Richland x Mandell	1512	44.5	13	34.7	17	35.5	14	38.2	14
Richland x B.H.Manchu	1516	45.4	6	34.1	21	35.1	16	38.2	14
Richland x Mandarin 507	1517	42.3	20	31.1	25	35.7	8	36.4	23
Richland x Linman 533	1518	44.9	11	36.9	8	36.1	7	39.3	7
Richland x Wis.Manchu #3	1519	45.4	6	36.1	14	36.5	4	39.3	7
Manchuria 13-177 x Richland	2715	48.1	1	36.9	8	33.4	22	39.4	5
L34R12 x Richland	2815	47.4	3	37.2	5	35.6	9	40.1	2
L6-12 x Richland	2915	45.2	8	36.6	12	34.6	19	38.8	10
Lincoln x Richland	3015	45.2	8	34.6	18	36.7	3	38.8	10
P.I.30600-2 x Richland	3115	43.4	15	39.2	2	35.6	9	39.4	5
P.I.65346 x Richland	3215	41.3	24	37.9	3	37.8	1	39.0	9
P.I.68474 x Richland	3315	42.6	19	34.4	20	34.9	17	37.3	21
Richland x P.I.68474-1	1534	46.3	4	34.6	18	35.6	9	38.8	10
P.I.79885 x Richland	3515	42.3	20	34.1	21	33.1	24	36.5	22
P.I.88298 x Richland	3615	43.0	17	37.4	4	35.2	15	38.5	13
P.I.89009-2 x Richland	3715	41.6	23	33.0	23	31.7	25	35.4	25
P.I.91161 x Richland	3815	44.8	12	39.3	1	36.3	5	40.1	2
P.I.92592 x Richland	3915	42.2	22	36.8	10	35.6	9	38.2	14
P.I.92608 x Richland	4015	42.7	18	36.7	11	34.3	21	37.9	19
P.I.92611 x Richland	4115	38.2	25	36.3	13	34.6	19	36.4	23
P.I.92707 x Richland	4215	43.3	16	35.0	16	36.3	5	38.2	14
P.I.92717 x Richland	1543	43.7	14	33.0	23	35.6	9	37.5	20
Lincoln		52.8		41.8		39.9		44.8	
Richland		39.7		33.3		35.7		36.2	
Mukden		41.0		35.4		35.1		37.1	

average seed yields of the varieties that were obtained. Lincoln was the highest yielding variety each year. Richland and Mukden were among the poorest yielding entries in each test except the bulk F_4 test in 1945, when they were near the midpoint of the yield array. As an average for the three years, Lincoln ranked first, Mukden second, and Richland third in yield. Variety test plots at Ames over a period of years have shown similar differences in yield among the three varieties.

The differences in yield among the varieties and bulk populations of the crosses were highly significant in each test and in the combined test, as shown by the analyses of variance in Table 5. The average yield of all entries varied considerably among years, because of seasonal fluctuations in the environment. One of the more important features of the combined analysis from the standpoint of bulk yield testing was the highly significant interaction of crosses and varieties with generations. This indicated that the relative differences in yield among the crosses and varietiec were not the same from generation to generation (year to year). Certain of the crosses, e.g. Mukden x Richland and L34R12 x Richland were relatively high in yield in each test. P.I. 79885 x Richland and P.I. 89009-2 x Richland, on the other hand, were consistently low in yield. Other crosses, however, varied considerably in yield rank from year to year. The cross, Manchuria 13-177 x Richland, was first in yield rank in the bulk F_2 test, eighth in the bulk F_3 test, and twenty-second in the bulk F_4 test. Conversely, P.I. 65346 x Richland was twenty-fourth

Table 5. Analyses of variance of yields and coefficients of variation for bulk F_2, F_3, and F_4 yield tests of twenty-five soybean crosses and three check varieties grown in successive years.

Source of variation	D.F.	Mean squares: Bulk F_2 generation 1943	Bulk F_3 generation 1944	Bulk F_4 generation 1945	Combined 1943 to 1945
Replications	5,5,5,15	64.74	18.17	47.32	43.41
Crosses and varieties 1/	29	67.63**	36.58**	17.86**	82.53**
Generations (years)	2				4,334.90**
Crosses and varieties x generations	58				19.77**
Experimental error	145,145,145,435	13.00	8.71	7.55	9.74
Coefficient of variation		8.1%	8.2%	7.7%	8.1%

1/ Of the varieties, Lincoln and Richland were entered twice and Mukden once in each test.

** Significant at the 1% level.

in 1943, third in 1944, and first in 1945. Although the latter two crosses were the extremes for this type of comparison, several others performed in a similar manner. The results with this group of bulk crosses certainly would leave some doubt as to the feasibility of relying upon a bulk yield test of the F_2 generation alone for measuring differences in yield performance among bulk populations of soybean crosses.

Another important feature was apparent when these results were compared with those obtained in the F_1 generation for four of the crosses. In the F_1 generation Mukden x Richland seemed to be the poorest and P.I. 89009-2 x Richland one of the best in respect to yield. The situation was reversed, however, in the bulk population tests of the same four crosses, where Mukden x Richland was the best and P.I. 89009-2 x Richland the poorest in yield in each generation. Several reasons for this reversal in performance may be postulated. One was that there possibly was an interaction between the two methods of planting, since the F_1 generation was space-planted and the segregating populations drilled. Another was the probable difference in the experimental accuracy of the results. A third postulation was that the degree of dominance and the extent of segregation for yield genes was variable among the crosses. Very probably all of these factors influenced the performance of the crosses to some extent at the successive generations studied.

Differences in combining ability among various varieties and strains of soybeans previously has received little study in hybridization work with this crop. Consequently, parents for crosses have been selected primarily on the basis of their performance in test plots rather than on a combination of performance and known breeding prepotency. The yields of the bulk populations of Lincoln x Richland and Mukden x Richland provided some interesting information on combining ability. Since Richland was a common parent to both crosses, the yields of the bulk populations of these crosses might be used as an indication of the contributions of the Mukden and Lincoln parents to the crosses. Lincoln has consistently outyielded Mukden in varietal test plots at Ames, although the two varieties are very similar in other important agronomic characteristics. It was expected, therefore, that the bulk populations of Lincoln x Richland would be higher yielding than those of Mukden x Richland. The results, however, were not in agreement with this expectation. Each of the bulk generations of Mukden x Richland outyielded those of Lincoln x Richland. The differences became smaller, however, with each successive generation. When compared with the parental yields, Lincoln x Richland was lower than the mean of the two parents in each bulk test, while Mukden x Richland was above the yield of the higher yielding parent. These results indicated that the combining ability for yield of Mukden with Richland was better than that of Lincoln with Richland. Similar differences in combining ability probably existed among the other parents but could not be evaluated in this way because all parents were not included in the bulk tests.

Maturity

Time of maturity is an agronomic character of considerable importance in soybeans. Varieties that mature about the time of the first killing frost in the fall in any locality usually yield more on the average than those which mature either sooner or later. Consequently, it is an important factor in the evaluation of segregating populations.

The mean dates of maturity of the bulk F_2, F_3, and F_4 generations of the twenty-five crosses and three varieties appear in Table 6. The average maturity of all entries was about the same in 1943 and 1944 but, because of a cool wet spring, approximately a week later in 1945. Differences between the bulk crosses in time of maturity were evident in each generation and remained fairly consistent from year to year. Although the method used to measure maturity was biased towards the later side, the maturities of the bulk populations were somewhat indicative of the relative proportions of early, medium, and late types in each cross. As an example, the bulk generations of cross No. 1517 were composed primarily of plants earlier than Richland, which was the later of the two parents.

The same crosses used to indicate differences in combining ability for yield among the parental varieties can be used for the same purpose with maturity. The bulk generations of cross No. 1415

Table 6. Mean dates of maturity of bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses and three check varieties grown in successive years.

Cross number or variety1/	Bulk F_2 1943	Bulk F_3 1944	Bulk F_4 1945	Average 1943 to 1945
1115	9-30	9-29	10-10	10-3
1315	10-3	10-4	10-12	10-6
1415	9-23	9-27	10-6	9-29
1512	10-2	10-3	10-12	10-5
1516	10-1	9-30	10-10	10-4
1517	9-13	9-10	9-24	9-16
1518	9-26	9-26	10-7	9-29
1519	9-26	9-25	10-6	9-29
2715	10-6	10-5	10-14	10-8
2815	10-3	10-5	10-13	10-7
2915	10-2	10-5	10-12	10-6
3015	10-3	10-6	10-12	10-7
3115	9-29	9-26	10-7	10-1
3215	9-28	9-27	10-8	10-1
3315	9-28	9-26	10-9	10-1
1534	10-3	10-3	10-13	10-6
3515	9-27	9-26	10-7	9-30
3615	9-28	9-27	10-8	10-1
3715	10-2	10-6	10-14	10-7
3815	9-29	9-27	10-9	10-1
3915	9-29	9-27	10-7	10-1
4015	9-28	9-26	10-9	10-1
4115	9-28	9-27	10-8	10-1
4215	10-1	9-28	10-11	10-3
1543	10-3	10-2	10-11	10-5
Lincoln	9-30	9-27	10-7	10-1
Richland	9-20	9-18	9-30	9-23
Mukden	9-26	9-26	10-9	9-30

1/ Parentage of crosses appears in Table 4.

were similar to the later parent in average maturity. The bulk populations of cross No. 3015, however, were definitely later than Lincoln, the later parent. If the parents had been included, cross No. 2715 probably would have been slightly earlier in average maturity than the later parent and cross Nos. 3515 and 3715 somewhat later than the later parent in the same respect. These possibilities would have been in accord with the postulations based on the maturity measurements made in the F_1 generations of these crosses. Maturity readings in the early generations of bulk soybean crosses, therefore, appear reasonably indicative not only of the maturity composition of the populations of each cross but also of the genotype of the parents.

Height

Certain varieties of soybeans, when grown in Iowa, are too short to harvest satisfactorily with a combine. This is one of the disadvantages of Richland when grown on lighter soils. It is desirable, therefore, to develop varieties tall enough so that all pods on the lower parts of the stems can be harvested. As shown in Table 7, all bulk crosses were taller than the Richland parent in average plant height. Almost half of them were about as tall as Lincoln and Mukden, varieties with a satisfactory height for combining. A few, however, were only an inch or two taller than Richland in average height.

The results obtained with four of these crosses in the space-planted F_1 generation showed that cross No. 3715 was the only one

Table 7. Mean heights in inches of bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses and three check varieties grown in successive years.

Cross number or variety1/	Bulk F_2 1943	Bulk F_3 1944	Bulk F_4 1945	Average 1943 to 1945
1115	46	37	39	40
1315	48	38	38	41
1415	43	37	39	40
1512	46	37	41	41
1516	46	36	39	40
1517	38	27	38	34
1518	41	33	38	37
1519	41	34	38	38
2715	49	37	36	41
2815	44	37	39	40
2915	44	37	39	40
3015	47	38	40	42
3115	44	34	36	38
3215	39	33	34	35
3315	40	32	36	36
1534	38	33	37	36
3515	38	30	34	34
3615	41	34	36	37
3715	43	36	37	39
3815	43	35	37	39
3915	43	34	36	38
4015	42	34	35	37
4115	40	34	39	37
4215	44	35	37	39
1543	45	36	39	40
Lincoln	47	37	40	41
Richland	36	28	35	33
Mukden	47	38	41	42

1/ Parentage of crosses appears in Table 4.

which exceeded both parents in average plant height. The other three were intermediate between the two parents in the same respect. The average heights of the same crosses in the bulk tests agreed quite well with the F_1 expectations. Cross No. 1415 was intermediate between the two parents in height in each bulk test. Cross No. 3715, on the other hand, was definitely taller than Richland, the taller of the two parents, in each generation from the bulk F_2 to the bulk F_4. In this case height differences among the crosses, as measured in the F_1 generation, were related to the average performance of the subsequent bulk generations.

<u>Lodging score</u>

Lodging, like plant height, is an important factor in combine harvesting of the soybean crop. Difficulties are measurably increased when lodging susceptible varieties are grown on the fertile soil types. It was primarily because of its high degree of lodging resistance that Richland was selected as the common parent for these crosses. As indicated by the lodging scores in Table 8, the bulk populations of the crosses differed in ability to stand up. Although only one of the crosses lodged less than Richland, most of them were no more lodging susceptible than Mukden. The lodging resistance of Mukden has generally been better than most other parental varieties of the twenty-five crosses in variety test plots at Ames.

Table 8. Mean lodging scores of bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses and three check varieties grown in successive years.

Cross number or variety[1/]	Bulk F_2 1943	Bulk F_3 1944	Bulk F_4 1945	Average 1943 to 1945
1115	3.0	1.2	2.7	2.3
1315	3.0	1.8	2.8	2.6
1415	2.8	1.0	2.2	2.0
1512	3.0	1.2	2.7	2.3
1516	3.0	1.5	2.8	2.4
1517	2.0	1.0	1.0	1.3
1518	3.0	1.5	2.2	2.2
1519	3.0	1.5	2.2	2.2
2715	3.8	1.8	3.0	2.9
2815	3.0	1.5	2.8	2.4
2915	3.0	1.5	2.8	2.4
3015	3.0	1.3	2.5	2.3
3115	3.0	1.7	2.5	2.4
3215	3.2	1.3	2.8	2.4
3315	3.2	1.2	2.5	2.3
1534	3.3	1.7	3.0	2.7
3515	3.2	1.0	2.7	2.3
3615	3.0	1.5	2.3	2.3
3715	3.0	1.3	3.2	2.5
3815	3.3	1.5	2.8	2.6
3915	3.0	1.0	2.2	2.1
4015	3.3	1.3	2.7	2.4
4115	3.5	1.3	2.5	2.4
4215	3.0	1.3	2.7	2.3
1543	3.0	1.3	2.5	2.3
Lincoln	3.0	1.9	2.8	2.6
Richland	2.7	1.0	1.3	1.7
Mukden	2.8	1.2	3.2	2.4

1/ Parentage of crosses appears in Table 4.

In the bulk tests the cross, Manchuria 13-177 x Richland (cross No. 2715) was the poorest in lodging resistance, while Mukden x Richland (cross No. 1415) was one of the best. The bulk populations of cross Nos. 3515 and 3715 were intermediate among the crosses for lodging score. Most of the bulk crosses contained a sufficient number of plants with good lodging resistance to enable effective selection for this character in the bulk populations included in the study.

Correlations

Correlations among the bulk generations of the crosses were calculated for each of the four agronomic characters studied to obtain a measure of the consistency in performance in consecutive years. These correlations are shown in Table 9. None for yield approached

Table 9. Correlation coefficients for mean yields, maturities, heights, and lodging scores among bulk F_2, F_3, and F_4 generations of twenty-five soybean crosses grown in successive years.

Bulk generations and years	D.F.	Yield	Maturity	Height	Lodging score
F_2 1943 and F_3 1944	23	.1995	.9306**	.8423**	.4300*
F_2 1943 and F_4 1945	23	.1495	.9644**	.4581*	.7333**
F_3 1944 and F_4 1945	23	.2899	.9583**	.5142**	.4545*

* Significant at the 5% level.
** Significant at the 1% level.

significance. Those for the other characters, however, all were statistically significant. The results for any one generation apparently were a poor indication of differences in yield performance among the bulk populations of the crosses. Differences in maturity, height, and lodging, on the other hand, were evaluated with reasonable accuracy in any one of the bulk generations.

1945 bulk F_3 test

An additional bulk yield test of the F_3 generations of the four crosses selected for study on a pedigree basis was grown in 1945. The same varieties used in previous bulk tests were included as checks. The mean agronomic results obtained in this test are presented in Table 10. The analysis of variance of the yields and the

Table 10. Mean yields, maturities, heights, and lodging scores of the bulk F_3 generations of four soybean crosses grown in 1945 with three check varieties.

Cross number or variety1/	Yield (Bushels per acre)	Date of maturity	Height in inches	Lodging score
1415	34.4	10-7	38	2.7
2715	36.9	10-14	36	3.2
3515	34.8	10-7	32	2.8
3715	31.0	10-13	37	3.2
Lincoln	38.8	10-8	39	2.5
Richland	36.3	9-30	36	1.2
Mukden	34.8	10-8	40	2.8

1/ Parentage of crosses appears in Table 4.

coefficient of variation appear in Table 11. As the mean yields of the crosses varied more than the mean yields of the varieties, little would have been gained by partitioning the mean squares for crosses and varieties and experimental error into their component parts.

Table 11. Analysis of variance of the yields and the coefficient of variation for the bulk F_3 test of four soybean crosses and three check varieties grown in 1945.

Source of variation	D.F.	Mean square
Replications	5	17.52
Crosses and varieties	6	35.45**
Experimental error	30	3.89
Coefficient of variation		5.6%

** Significant at the 1% level.

In this test the relative differences among the crosses and varieties for maturity, height, and lodging score were very similar to those found in the other bulk population trials. The yields of the three check varieties also were about the same as in the bulk F_4 test conducted that year. Differences in yield among the bulk F_3 populations of the crosses, however, were not the same, except for cross No. 3715.

Cross No. 2715 was the highest of the four crosses in yield in this test. Cross Nos. 1415 and 3515 were intermediate in yield and cross No. 3715 was the lowest in yield. These results further substantiated the inconsistencies in yield performance of the bulk populations at successive generations and in different years.

F_2 Generation Spaced Plant Study

Among plant breeders the pedigree method of handling segregating populations of crosses in self-pollinated crops is used more commonly than the bulk method. The selection of desirable plants in the F_2 generation is generally based on visual observations of the characteristics of each plant. Characters which are simply inherited usually can be easily selected. Characters inherited in a complex manner, on the other hand, are difficult to select for, since the environment may mask the true expression of the genotype of a plant. Most plant breeders select only the most vigorous, high yielding F_2 plants which appear satisfactory for time of maturity, plant height, and other characters within each cross. This practice, in light of the probable effects of environment on plant phenotypes, raises the question as to its value in a breeding program. In other words, are observed differences for such complex characters as yield, maturity, and height among spaced F_2 plants of a cross primarily of an environmental nature or of a genetic nature due to segregation? The greater the effects of the environment, the less will be the breeding value of visual selection for these characters. The pedigree studies reported herein were conducted in an attempt to gain further information on this problem as it relates to selection in segregating populations of soybean crosses.

Measurements for seed yield, maturity, and height were made individually on 100 consecutive competitive spaced plants in each of three varieties and in the F_2 generation of each of four crosses. The frequency distributions of the seed yields per plant for these crosses and varieties are found in Table 12. The mean, standard deviation, and coefficient of variation for each distribution also are included. The means were not comparable, since there were no replications, but the distributions and their standard deviations provided interesting comparisons among the crosses and varieties. Although the range in seed yield was greater for each of the crosses than for any of the three varieties, the differences were not nearly as large as was expected. These relatively small differences were substantiated by the standard deviations and coefficients of variation, which were not much larger for two of the crosses than for the varieties. The other two crosses, however, were about twice as variable for seed yield per plant as the varieties. These results indicated that a major portion of the variability in seed yield among the F_2 plants of each cross was due to the environment rather than to genetic causes. Selection for

Table 12. Frequency distributions for seed yields per plant of 100 consecutive competitive plants in the F_2 generations of each of four soybean crosses and in each of three varieties with their means, standard deviations, and coefficients of variation.

Seed yield in grams per plant (Class center)	Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)	Richland	Mukden	Lincoln
5			1				
10		2	1	2		2	
15	1	2	4	12		6	
20	5	1	10	7	1	11	5
25	6	7	14	6	4	17	5
30	11	2	14	13	8	14	11
35	8	12	18	6	14	17	24
40	10	7	12	12	20	13	19
45	14	12	12	7	20	15	11
50	16	8	4	6	14	3	11
55	6	7	5	4	9	2	6
60	10	14	4	11	7		3
65	7	4	1	1	1		2
70	3	10	1	5	2		2
75	2	3	1	2			
80	1	3		1			
85		2		2			1
90		2		3			
95		2					
Mean	45.26	51.60	35.15	41.49	43.64	32.35	40.48
Standard deviation	14.50	19.06	13.06	20.49	10.19	10.27	11.81
Coefficient of variation	32.0%	36.9%	37.1%	49.4%	23.3%	31.7%	29.2%

differences in yielding ability among these plants, therefore, probably would not have been too valuable from a genetic standpoint.

Time of maturity is an agronomic character of soybeans which generally is not affected as much by the environment as is yield. As shown by the frequency distributions in Table 13, the range in maturity of the F_2 plants in each cross was greater than that of the plants in any variety. Differences in maturity among the F_2 plants of each cross apparently were affected more by genetic segregation than the differences in yield, as indicated by the relative sizes of the standard deviations in comparison with the varieties. Consequently, selection for maturity differences among the F_2 plants of each cross might have been of more value genetically than selection for differences in yielding ability.

The frequency distributions and their statistical constants for plant heights in inches of each F_2 cross and variety appear in Table 14. In general, there was somewhat less variability for plant height among the crosses and varieties than there was for maturity. The coefficients of variation of the height distributions for two of the crosses were not greatly different than those of the varieties. The heights for the other two crosses, however, were more than twice as variable as those for the varieties. In the latter two crosses, namely, cross Nos. 3515 and 3715, genetic segregation probably accounted for a greater proportion of the total variation for height than it did for yield. The range in plant height among the F_2 plants of cross No. 3715 indicated that a certain amount of transgressive

Table 13. Frequency distributions for dates of maturity of 100 consecutive competitive plants in the F_2 generations of each of four soybean crosses and in each of three varieties with their means, standard deviations, and coefficients of variation.

Date of maturity (Class center)	Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)	Richland	Mukden	Lincoln
August 31			1				
September 5		1	5	4			
September 10		9	15	4			
September 15	13	15	37	13	11	7	
September 20	22	10	15	2	49	32	13
September 25	37	15	16	15	38	42	58
September 30	24	9	7	39	2	17	29
October 5	2	13	3	11		2	
October 10	2	17	1	9			
October 15		8		3			
October 20		2					
October 25		1					
Mean	9-24	9-29	9-18	9-27	9-22	9-24	9-26
Standard deviation	5.36	11.60	7.37	9.26	3.16	4.00	2.75
Coefficient of variation	21.9%	40.7%	40.7%	34.1%	14.6%	16.8%	10.5%

Table 14. Frequency distributions for plant heights in inches of 100 consecutive competitive plants in the F_2 generations of each of four soybeans crosses and in each of three varieties with their means, standard deviations, and coefficients of variation.

Plant height in inches (Class center)	Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)	Richland	Mukden	Lincoln
5				1			
10			5	4			
15			27	14			
20	1		31	9	5		
25	13	4	18	10	71	12	4
30	24	22	16	26	24	23	23
35	38	45	3	23		54	56
40	20	29		12		11	15
45	3			1			2
50	1						
Mean	34.08	34.98	20.96	28.13	25.90	33.07	34.86
Standard deviation	5.15	4.00	5.93	9.02	2.36	4.07	3.41
Coefficient of variation	15.1%	11.4%	28.3%	32.0%	9.1%	12.3%	9.8%

segregation occurred for this character, since Richland was the taller of the two parents. In fact, the F_2 plant results with this cross agreed very closely with the suppositions made about its height potentialities on the basis of the spaced F_1 plant and bulk population tests. An unexpected result in the F_2 plant study was the relatively narrow range for plant height in cross No. 2715. The two parents of this cross differed widely in plant height and the same F_2 plants were among the most variable of the four crosses for yield and maturity. For these reasons, a greater range in plant height was expected.

The 100 spaced F_2 plants per cross measured for their agronomic characteristics constituted a reasonably random sample of the F_2 population of plants in each of the crosses. As the crosses were not replicated, the plants were grown and harvested under conditions similar to those usually encountered in making plant selections in segregating populations. The common practice of selecting only the better yielding plants in the segregating populations of crosses did not seem justified on the basis of the results secured in this study. If these samples of F_2 plants were truly an indication of the extent of variability for seed yield among all plants of the F_2 populations, random selection of plants probably would have been about as successful in the attainment of high yielding genotypes in these populations as the selection of high yielding plants. Replicated progeny tests of most of these plants were grown in the F_3 generation the next year to obtain additional information on the breeding behavior of the F_2 generation. The F_3 generation results are presented and discussed in the succeeding section.

F_3 Line Test

In the previous section it was shown that the environment appeared to have a pronounced effect on phenotypic differences among the F_2 plants of the four soybean crosses included in this investigation. If the usual pedigree method of breeding had been continued, the seed from the most desirable appearing F_2 plants would have been planted in progeny rows the succeeding year. Here again the environment probably would have influenced the expression of agronomic differences among the lines.

Most of the F_2 plants in each cross included in this study produced sufficient seed for replicated progeny tests. Progenies of seventy-seven of the F_2 plants per cross were planted in 1945 to study their breeding behavior in the F_3 generation. This procedure made possible a more accurate appraisal of the agronomic differences among the F_3 lines than the usual pedigree method. It also made possible a comparison of the characteristics of the individual F_2 plants and the means of their replicated progenies in the F_3 generation.

Yield

As shown by the analyses of variance of the seed yields of the seventy-seven F_3 lines, parents, and bulk F_2 and F_3 generations in each of the four crosses in Table 15, the mean yield differences among the entries were highly significant in three of the four crosses. In the fourth cross the differences approached significance. The frequency distributions of the mean yields of the F_3 lines in each of the crosses, however, showed that only a few of the lines were significantly higher or lower in yield than Richland. These distributions are recorded in Table 16. Since Richland generally has yielded less than the other parents of these crosses in most replicated tests at Ames, these results indicated that the opportunities for selecting lines superior in yield to the parents did not appear very promising.

The yield results in this test did not agree very well with those obtained in the bulk population trials of the same crosses. The bulk F_3 generations of cross Nos. 1415 and 2715 were slightly below Richland in seed yield in this test. Those of cross Nos. 3515 and 3715 were slightly above. In the bulk population studies, on the other hand, cross Nos. 1415 and 2715 generally were well above Richland in yield, while cross Nos. 3515 and 3715 yielded about the same as Richland. The frequency distributions of the yields of the F_3 lines, furthermore, showed no superiority in yield of cross No. 2715 over that of cross No. 3515. Cross No. 3715, which was the lowest yielding of the four crosses in the bulk tests, actually appeared to have a more favorable yield distribution of F_3 lines than either cross No. 2715 or cross No. 3515. The relative yield performance of cross No.

Table 15. Analyses of variance of seed yields of seventy-seven F_3 lines, parents, and bulk F_2 and F_3 generations in each of four soybean crosses.

Source of variation	D.F.	Mean squares: Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 88009-2 x Richland (Cross No. 3715)
Replications	2	946.26	82.72	356.23	1,504.08
Blocks (eliminating lines)	24	25.06	30.73	19.40	27.97
Lines (ignoring blocks)	80	25.26**	61.12**	35.13**	22.87
Error (intrablock)	134,134 136,136	10.17	18.53	13.01	14.92
Error (randomized complete block)	158,158 160,160	12.43	20.39	13.97	16.88
General mean in bushels per acre		44.6	44.2	47.7	40.2
Precision		112.2%	103.9%	102.3%	105.8%
Coefficient of variation		7.5%	10.0%	7.7%	9.9%
Average standard error of a difference		2.72	3.62	3.02	3.26

** Significant at the 1% level.

Table 16. Frequency distributions of mean seed yields of seventy-seven F_3 lines and the bulk F_3 generations in each of four soybean crosses, as compared to the yield of Richland.

Cross	Class centers of minus 3.5 to plus 3.5 times the average standard error of a difference							
	-4 to -3	-3 to -2	-2 to -1	-1 to 0	0 to +1	+1 to +2	+2 to +3	+3 to +4
Mukden x Richland (Cross No. 1415)			8	22	29	14	3	1
Bulk F_3 generation				1				
Manchuria 13-177 x Richland (Cross No. 2715)	1	4	7	31	18	14	2	
Bulk F_3 generation				1				
P.I. 79885 x Richland (Cross No. 3515)	1	5	12	28	20	10	1	
Bulk F_3 generation					1			
P.I. 89009-2 x Richland (Cross No. 3715)			3	23	32	18	1	
Bulk F_3 generation					1			

1415, however, was very similar in the bulk and pedigree tests when the same type of comparison was made. It was also of interest to note that cross No. 3715, which had the greatest standard deviation of all crosses for seed yield in the F_2 spaced-plant study (see Table 12), had the lowest and only non-significant mean square for lines in this F_3 test.

Each replication of the four crosses in this test was randomized first on a whole cross basis so that the mean seed yields of the crosses could be compared. These general means are found in

Table 15. The chance placement of the replications of cross No. 3515 on the more fertile parts of the experimental area, as shown by the higher yield of Richland in this group, resulted in this cross having the highest mean yield of the four crosses. As the replications of the other crosses were affected favorably in some instances and unfavorably in others by their placement in the field, these general means among the crosses could not be validly compared.

Maturity

Maturity differences among the F_3 lines were much more striking than the yield differences. The frequency distributions of the mean dates of maturity, presented in Table 17, showed that all four of the crosses contained F_3 lines earlier and later than either parent. The extent of transgressive segregation for factors conditioning maturity was greatest for cross No. 3515. The range in maturity among the F_3 lines was smallest for cross No. 1415. Consequently, it had the smallest mean square for lines of the four crosses, as shown by the analyses of variance of the maturities in Table 18. The F_3 lines in cross No. 2715, on the other hand, had the greatest range in maturity and the largest mean square for lines. Cross Nos. 3515 and 3715 were intermediate for maturity range and line mean square. These results conformed with the maturity measurements made on the parental F_2 plants of these lines (see Table 13), where cross No. 1415 had the lowest and cross No. 2715 the highest

Table 17. Frequency distributions of mean dates of maturity of seventy-seven F_3 lines, parents, and the bulk F_3 generations in each of four soybean crosses.

Cross or parent	Dates of maturity (Class centers) 9-20	9-23	9-26	9-29	10-2	10-5	10-8	10-11	10-14	10-17
Mukden x Richland										
(Cross No. 1415)		1	5	11	37	16	5	2		
Richland				1						
Mukden						1				
Bulk F_3 generation						1				
Manchuria 13-177 x Richland	2	2	6	3	12	6	5	29	10	2
(Cross No. 2715)										
Richland				1						
Manchuria 13-177								1		
Bulk F_3 generation								1		
P.I. 79885 x Richland										
(Cross No. 3515)	1	5	7	16	21	9	13	5		
Richland				1						
P.I. 79885					1					
Bulk F_3 generation						1				
P.I. 89009-2 x Richland		1	5	1	3	4	14	44	5	
(Cross No. 3715)										
Richland				1						
P.I. 89009-2								1		
Bulk F_3 generation								1		

Table 18. Analyses of variance of dates of maturity of seventy-seven F_3 lines, parents, and bulk F_2 and F_3 generations in each of four soybean crosses.

Source of variation	D.F.	Mean squares: Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)
Replications	2	603.72	59.12	40.77	207.69
Blocks (eliminating lines)	24	3.14	8.48	4.48	7.01
Lines (ignoring blocks)	80	31.22**	129.45**	69.66**	60.89**
Error (intrablock)	136	1.98	1.64	1.91	2.65
Error (randomized complete block)	160	2.16	2.67	2.29	3.30
General mean date of maturity		10-2	10-7	10-2	10-9
Precision		103.3%	145.1%	110.6%	113.8%
Coefficient of variation		4.5%	3.7%	4.5%	4.4%
Average standard error of a difference		1.2	1.1	1.2	1.4

** Significant at the 1% level.

standard deviation for maturity among the one hundred F_2 plants in each cross. Similarly, cross Nos. 3515 and 3715 each had an intermediate standard deviation for maturity among their F_2 plants.

The low coefficients of variation and average standard errors of a difference (Table 18) indicated that the maturity differences among the F_3 lines in each cross were evaluated with considerable accuracy. The opportunities for selecting F_3 lines from these crosses that were significantly different in maturity, therefore, appeared very good.

The results obtained in this F_3 line study also provided information on the breeding behavior for maturity of the early segregating generations. The average dates of maturity for each of the crosses, as shown in Table 18, indicated that cross Nos. 2715 and 3715 contained greater proportions of later maturing F_3 lines than the other two crosses. The frequency distributions of the maturities of the F_3 lines substantiated this indication. The same relative differences in maturity among these crosses were obtained in the F_1 generation, the bulk population tests, and the F_2 generation. Breeding behavior for maturity on a cross basis, therefore, seemed relatively consistent during the early generations following hybridization.

Height

Plant height was the third agronomic character measured in this test. The frequency distributions of the mean heights in inches of the F_3 lines, parents, and bulk F_3 generations in each of the four crosses appear in Table 19. As shown, the total range in height among the F_3 lines was about the same for each cross. Cross No. 3515, however, definitely had the greatest number of short lines and cross No. 1415 the greatest number of tall lines. Cross Nos. 2715 and 3715 were intermediate in this respect. The mean height in inches of all entries for each cross, given in Table 20, substantiated these statements. The bulk F_3 generation was intermediate in height to the two parents in three of the four crosses. In the fourth cross, cross No. 3715, it was significantly taller than Richland, the taller of the two parents. These results agreed quite well with the postulations made about plant height differences among these crosses based on the F_1 generation and the bulk population tests. The F_3 lines in cross No. 2715, however, averaged somewhat shorter than expected on the basis of the previous data.

Analyses of variance of the heights of the F_3 lines, parents, and bulk generations in each of the four crosses (Table 20) showed that the mean differences in height among the F_3 lines were highly significant in each cross. Although the F values for the line mean squares of height were smaller than the comparable ones of maturity, they were considerably larger than the comparable ones of yield. The coefficients of variation and the average standard errors of a difference of the heights indicated that the height differences among the F_3 lines were evaluated quite accurately. Effectiveness of

Table 19. Frequency distributions of mean heights in inches of seventy-seven F_3 lines, parents, and the bulk F_3 generations in each of four soybean crosses.

	Height in inches																		
Cross or parent	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Mukden x Richland (Cross No. 1415)						1	3	4	4	5	5	11	10	10	12	7	2	1	2
Richland										1									
Mukden														1					
Bulk F_3 generation												1							
Manchuria 13-177 x Richland (Cross No. 2715)			1		2	1	2	4	7	13	19	10	12	5	1				
Richland										1									
Manchuria 13-177											1								
Bulk F_3 generation										1									
P.I. 79885 x Richland (Cross No. 3515)	2	7	9	6	11	11	12	9	4	2	2	1	1						
Richland									1										
P.I. 79885	1																		
Bulk F_3 generation							1												
P.I. 89009-2 x Richland (Cross No. 3715)			3	1	4		6	2	3	5	12	10	9	15	5	2			
Richland								1											
P.I. 89009-2					1														
Bulk F_3 generation												1							

Table 20. Analyses of variance of heights in inches of seventy-seven F_3 lines, parents, and bulk F_2 and F_3 generations in each of four soybean crosses.

Source of variation	D.F.	Mean squares: Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)
Replications	2	420.16	138.53	59.41	78.73
Blocks (eliminating lines)	24	8.97	3.18	4.23	4.15
Lines (ignoring blocks)	80	26.74**	14.40**	20.47**	33.27**
Error (intrablock)	136	3.32	2.24	2.63	3.27
Error (randomized complete block)	160	4.17	2.38	2.87	3.40
General mean height in inches		37.8	35.7	30.8	36.0
Precision		114.9%	101.7%	103.2%	100.9%
Coefficient of variation		5.1%	4.3%	5.4%	5.1%
Average standard error of a difference		1.6	1.3	1.4	1.5

** Significant at the 1% level.

selection between F_3 lines for height, therefore, would have been about as good as for maturity.

Lodging score

Improved lodging resistance was one of the primary reasons for making this group of soybean crosses. It was desired to find, in the segregating populations, lines with lodging scores about as low as Richland. The frequency distributions of the mean lodging scores of the F_3 lines, parents, and bulk F_3 generations in each of the four crosses, as recorded in Table 21, showed that only a few lines in each cross had lodging scores as low or lower than Richland. A number of lines, however, exhibited more lodging resistance than the other parents. Transgressive segregation for factors affecting lodging susceptibility was somewhat more in evidence than transgressive segregation for factors affecting lodging resistance. Of the four crosses, cross Nos. 1415 and 3515 had the most lines with small lodging scores. Cross No. 2715, on the other hand, had the most lines with large lodging scores. These proportions were corroborated by the average lodging scores for all entries in each of the crosses, as shown in Table 22. These results, in turn, agreed with those obtained in the bulk population trials of the same crosses, where cross No. 1415 had the lowest and cross No. 2715 the highest average lodging score.

Table 21. Frequency distributions of mean lodging scores of seventy-seven F_3 lines, parents, and the bulk F_3 generations in each of four soybean crosses.

Cross or parent	Lodging scores (Class centers)										
	1.1	1.4	1.7	2.0	2.3	2.6	2.9	3.2	3.5	3.8	4.1
Mukden x Richland (Cross No. 1415)	3	3	11	16	16	15	6	4	3		
Richland				1							
Mukden						1					
Bulk F_3 generation					1						
Manchuria 13-177 x Richland (Cross No. 2715)	1	1	6	7	11	15	27	6	1	2	
Richland		1									
Manchuria 13-177							1				
Bulk F_3 generation								1			
P.I. 79885 x Richland (Cross No. 3515)	3	3	6	22	9	17	11	4		1	1
Richland		1									
P.I. 79885							1				
Bulk F_3 generation							1				
P.I. 89009-2 x Richland (Cross No. 3715)	3	1	6	8	11	27	18	3			
Richland		1									
P.I. 89009-2						1					
Bulk F_3 generation							1				

Table 22. Analyses of variance of lodging scores of seventy-seven F_3 lines, parents, and bulk F_2 and F_3 generations in each of four soybean crosses.

Source of variation	D.F.	Mean squares: Mukden x Richland (Cross No. 1415)	Mean squares: Manchuria 13-177 x Richland (Cross No. 2715)	Mean squares: P.I. 79885 x Richland (Cross No. 3515)	Mean squares: P.I. 89009-2 x Richland (Cross No. 3715)
Replications	2	20.17	2.01	1.39	14.82
Blocks (eliminating lines)	24	.37	.29	.32	.37
Lines (ignoring blocks)	80	.98**	.93**	1.07**	.76**
Error (intrablock)	136	.24	.20	.18	.19
Error (randomized complete block)	160	.26	.21	.20	.21
General mean lodging score		2.3	2.6	2.3	2.5
Precision		104.0%	101.9%	105.3%	105.0%
Coefficient of variation		21.7%	17.5%	19.0%	18.0%
Average standard error of a difference		.4	.4	.4	.4

** Significant at the 1% level.

The analyses of variance of lodging scores of the F_3 lines, parents, and bulk generations in each of the crosses are found in Table 22. The differences in mean lodging scores among the F_3 lines were highly significant in all cases. The F values for the line mean squares, however, did not approach the magnitude of the comparable ones for maturity and height. Lodging scores generally cannot be evaluated as accurately in the field as these characters. The high coefficients of variation of the lodging scores obtained in this test followed this generality. Improvements in lodging resistance over that of the more lodging susceptible parents, nevertheless, seemed a definite possibility on the basis of these results.

Correlations

It was shown by analyses of variance that the differences in mean yield, maturity, and height among the F_3 lines in each cross included in this study were highly significant with but one exception. Each F_3 line was the progeny of a single F_2 plant grown the previous year and measured for the same agronomic characters. The degree of association between the F_2 plants and their descendant F_3 lines for these characters was measured by the use of correlations. These plant-progeny correlations for each cross appear in Table 23. Two of the four correlations for yield were highly significant. They were so small, however, that most of the variation among the F_3 means was not attributable to regression. The correlations for maturity and for

Table 23. Parent plant-progeny correlations of yields, plant heights, and maturities of seventy-seven F_2 plants and the means of their replicated progenies in each of four soybean crosses.

Variates Correlated	D.F.	Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)
F_2 plant yield and F_3 mean yield	75	.3720**	.0733	.2226	.3001**
F_2 plant height and F_3 mean height	75	.6518**	.6997**	.7186**	.8162**
F_2 plant maturity and F_3 mean maturity	75	.8352**	.8837**	.8636**	.7894**

** Significant at the 1% level.

height, on the other hand, all were highly significant and large enough so that a considerably proportion of the variation among the F_3 means was due to regression. Differences in yield among the F_2 plants in these crosses, therefore, were of little or no value as a basis for selecting high yielding progenies. Breeding behavior for maturity and height, on the contrary, was reasonably consistent during the F_2 and F_3 generations.

F_4 Line Test

Visible segregation for agronomic characters generally continues through the F_4 or F_5 and sometimes the F_6 generations following hybridization in self-pollinated crops. In the F_6 generation pedigree lines usually are pure enough to be bulked for subsequent yield testing. It has been suggested by some breeders, however, that the genetic factors conditioning yield and other agronomic characters in soybeans are stable enough by the F_3 or F_4 generation to merit the evaluation of lines for these characters in replicated trials. If this supposition were true, the utilization of this procedure would enable the elimination of low yielding lines earlier than usual in the breeding program and thereby make more time available for selection in the more promising material in subsequent generations.

A substantial amount of genetic segregation for agronomic characters among F_2 plants in the soybean crosses included in this study was indicated by their progeny tests in the F_3 generation in

1945. The extent of segregation among F_3 plants was studied next. This was accomplished by growing F_3 progenies in a replicated test in the F_4 generation in 1946. The selection of lines for inclusion in this test was based on the yield distributions of the F_3 lines in 1945. In all, fifteen F_3 lines were selected from the yield distributions of each of the crosses. Each F_3 line thus selected was represented in the F_4 generation by the progenies of five of its F_3 plants. The parents and bulk F_3, F_4, and F_5 generations also were incorporated in the test for each cross, thereby making a total of eighty entries per cross. This procedure made it possible to analyze agronomic differences among F_4 lines within F_3 families and among the progenies of F_3 families within each cross. In addition, it provided a means for continuing the study of breeding behavior at successive generations in these crosses.

Yield

The seed yields of the F_4 lines, parents, and bulk generations in each cross were obtained on single eight foot rows replicated three times in a randomized split plot design in 1946. F_3 families constituted the whole plots and F_4 lines within F_3 families the sub-plots in the experimental design. Each replication of all entries in each cross also was randomized on a whole cross basis. The mean yields of the F_4 lines, parents, and bulk generations in each of the four crosses in comparison with the yields of the parental F_2 plants and

F_3 lines in 1944 and 1945, respectively, appear in Tables 24 to 27. These yield data showed several very noteworthy features. In the first place, most yield differences among the F_4 lines within each F_3 family were relatively small. Secondly, the range in yield of the progenies of F_3 families, as an average of the five F_4 lines in each, was considerably smaller than the range in yield of the parental F_3 lines in 1945. A final point of interest was the yield performance of the three bulk generations in each cross as compared to the two parents. All three bulk generations of cross No. 1415 yielded more than either parent. Their average yield superiority was 2.3 bushels per acre above Mukden, the higher yielding parent. In the other three crosses, however, only the bulk F_3 generation of cross No. 3715 outyielded both parents, while all others were intermediate to the parents. If these bulk generation yields were indicative of the continued manifestations of the degree of heterosis in these crosses, they were distinctly contradictory to the results obtained in the F_1 generation spaced plant study (see Table 1). In that study cross No. 1415 showed the least amount of heterosis of the four crosses.

The analyses of variance of the seed yields obtained in the 1946 test are given in Table 28. They offered further confirmation of some of the statements made in the previous paragraph. In only one of the crosses, namely, cross No. 3515, were the differences between the F_3 family progenies statistically significant. Yield differences among the parental F_3 lines were highly significant for every cross

Table 24. Seed yields of F_2 plants in 1944 and the mean yields of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 1415 (Mukden x Richland), together with the yields of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Yield in grams)	F_3 line (Bushels per acre)	F_4 lines (Bushels per acre)					
			1	2	3	4	5	Mean
1415-22	68	43.9	34.4	35.1	37.0	30.4	35.0	34.4
1415-25	56	48.7	36.5	35.5	36.4	35.4	34.2	35.6
1415-29	48	47.1	33.1	33.0	35.2	33.3	35.9	34.1
1415-30	57	50.0	37.4	36.2	36.1	31.5	36.4	35.5
1415-32	50	43.0	32.5	32.3	36.3	36.8	35.0	34.6
1415-42	64	45.3	34.5	33.5	37.6	33.3	36.7	35.1
1415-44	48	46.1	33.8	32.2	31.7	32.4	29.3	31.9
1415-50	52	47.7	34.6	35.0	36.3	35.7	35.9	35.5
1415-56	40	45.0	33.2	33.2	32.9	32.6	33.3	33.0
1415-57	32	44.2	36.2	35.8	36.8	37.7	37.2	36.7
1415-60	37	39.9	33.3	33.8	34.7	30.6	34.9	33.4
1415-63	54	42.7	33.6	39.6	36.5	36.6	33.5	35.9
1415-72	30	41.6	33.3	31.1	33.5	33.6	33.2	32.9
1415-74	72	45.5	36.0	29.5	33.2	39.0	35.9	34.7
1415-77	47	40.4	29.9	31.2	28.7	32.6	31.8	30.8

Mukden	Richland	Bulk F_3	Bulk F_4	Bulk F_5
32.7	31.9	36.1	32.9	36.0

Mean yield of all entries in 1946 test
34.3

Table 25. Seed yields of F_2 plants in 1944 and the mean yields of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 2715 (Manchuria 13-177 x Richland), together with the yields of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Yield in grams)	F_3 line (Bushels per acre)	F_4 lines (Bushels per acre)					
			1	2	3	4	5	Mean
2715- 4	39	44.1	38.5	38.2	29.9	37.9	37.9	36.5
2715-17	46	50.8	34.2	35.0	36.9	37.6	38.5	36.5
2715-23	72	46.3	36.9	37.5	37.2	41.7	38.5	38.4
2715-30	66	48.7	37.0	41.0	41.3	37.7	38.8	39.2
2715-31	37	39.7	35.9	35.6	35.5	36.9	37.2	36.2
2715-38	62	44.8	42.6	35.7	33.4	35.9	34.1	36.3
2715-40	57	53.3	37.0	33.6	37.0	36.3	38.5	36.5
2715-51	42	41.5	32.1	34.2	33.9	37.5	31.9	33.9
2715-56	45	44.1	31.4	34.0	33.6	35.9	37.3	34.5
2715-58	70	47.3	31.0	32.3	36.4	37.2	29.7	33.3
2715-63	55	42.6	40.3	38.7	39.1	40.1	38.2	39.3
2715-72	62	50.1	35.0	35.7	32.7	35.7	32.1	34.3
2715-76	46	43.7	40.3	37.8	35.2	38.5	34.7	37.3
2715-78	26	45.4	34.8	34.1	33.5	31.2	33.9	33.5
2715-80	25	42.8	36.5	35.0	36.3	34.9	34.1	35.3

Manchuria 13-177	Richland	Bulk F_3	Bulk F_4	Bulk F_5
40.3	35.2	38.8	40.2	36.9

Mean yield of all entries in 1946 test
36.2

Table 26. Seed yields of F_2 plants in 1944 and the mean yields of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3515 (P.I. 79885 x Richland), together with the yields of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Yield in grams)	F_3 line (Bushels per acre)	F_4 lines (Bushels per acre)					
			1	2	3	4	5	Mean
3515- 3	36	50.8	36.2	38.1	33.6	37.0	36.4	36.3
3515-16	34	49.4	37.6	37.3	39.7	36.7	37.5	37.8
3515-18	33	45.1	37.3	39.9	35.8	38.7	39.1	38.2
3515-29	70	51.7	35.5	32.7	38.1	33.7	29.5	33.9
3515-37	36	53.2	37.5	39.3	37.3	35.6	35.3	37.0
3515-44	47	46.3	33.5	37.5	34.1	32.2	39.0	35.3
3515-51	42	41.3	36.9	35.8	36.0	36.1	33.9	35.7
3515-67	37	49.7	36.4	34.8	35.1	36.6	36.4	35.8
3515-68	61	47.1	32.5	17.3	36.5	33.1	36.4	31.2
3515-73	41	47.9	35.8	33.7	39.0	38.5	34.0	36.2
3515-82	48	45.9	37.5	34.5	35.2	37.0	38.4	36.5
3515-88	42	46.5	34.0	32.4	27.8	32.5	33.9	32.1
3515-93	37	48.4	34.5	34.5	33.0	36.3	34.0	34.5
3515-95	31	43.4	34.4	35.4	39.1	38.2	36.4	36.7
3515-98	44	50.2	35.3	33.8	34.8	35.2	32.6	34.3

P.I. 79885	Richland	Bulk F_3	Bulk F_4	Bulk F_5
37.0	32.5	35.6	34.5	34.5

Mean yield of all entries in 1946 test
35.4

Table 27. Seed yields of F_2 plants in 1944 and the mean yields of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3715 (P.I. 89009-2 x Richland), together with the yields of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Yield in grams)	F_3 line (Bushels per acre)	F_4 lines (Bushels per acre)					
			1	2	3	4	5	Mean
3715-15	44	37.0	36.5	32.8	33.5	34.6	35.8	34.6
3715-18	29	40.5	39.0	34.4	39.1	38.2	38.4	37.8
3715-20	56	41.9	36.6	34.3	32.9	36.6	31.8	34.4
3715-23	29	42.5	31.8	31.2	31.4	35.0	31.9	32.3
3715-25	43	42.8	35.7	37.2	30.1	35.2	36.2	34.9
3715-26	42	40.9	34.5	32.0	32.4	29.4	30.9	31.8
3715-39	48	37.6	31.8	34.4	31.8	38.1	28.1	32.9
3715-48	30	39.5	32.6	31.0	31.8	33.8	34.6	32.8
3715-53	70	39.6	33.7	33.2	36.0	35.9	33.4	34.4
3715-68	32	35.7	32.0	37.1	37.8	33.5	33.8	34.8
3715-73	55	44.4	31.7	35.9	36.4	39.3	35.9	35.8
3715-76	87	44.8	32.6	39.4	32.2	34.2	34.8	34.7
3715-80	59	38.3	33.6	32.2	37.2	34.4	34.3	34.3
3715-83	39	40.1	36.3	34.7	37.1	36.5	36.8	36.3
3715-96	82	41.8	33.1	34.0	34.4	33.7	34.5	33.9

P.I. 89009-2	Richland	Bulk F_3	Bulk F_4	Bulk F_5
36.9	32.2	37.1	35.6	36.3

Mean yield of all entries in 1946 test
34.5

Table 28. Analyses variance of yields obtained in 1946 test of F_4 lines, parents, and bulk populations in each of four soybean crosses.

Source of variation	D.F.	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square
		(Mukden x Richland)		(Manchuria 13-177 x Richland)		(P.I. 79885 x Richland)		(P.I. 89009-2 x Richland)	
Whole Plot:									
Replications	2		750.90		50.58		663.63		194.26
F_3 family progenies	15		36.38		56.99		53.78**		35.80
Error (a)	30		20.64		31.40		14.98		26.59
Subplot:									
F_4 lines within F_3 families	64		10.37**		14.96**		22.02**		13.56**
	4	1415-22	17.58*	2715-4	40.92**	3515-3	8.27	3715-15	7.10
	4	" -25	2.52	" -17	9.59	" -16	3.87	" -18	11.40
	4	" -29	5.41	" -23	11.40	" -18	7.68	" -20	13.90*
	4	" -30	16.06*	" -30	10.81	" -29	30.84**	" -23	7.16
	4	" -32	13.30*	" -31	1.80	" -37	7.99	" -25	22.88**
	4	" -42	11.23	" -38	40.16**	" -44	24.95**	" -26	10.39
	4	" -44	7.86	" -40	9.88	" -61	3.54	" -39	40.76**
	4	" -50	1.31	" -51	15.11	" -67	3.12	" -48	6.40
	4	" -56	.25	" -56	15.01	" -68	190.00**	" -53	5.84
	4	" -57	1.74	" -58	33.36**	" -73	18.41*	" -68	18.93*
	4	" -60	8.94	" -63	2.55	" -82	7.73	" -73	22.10**
	4	" -63	19.25**	" -72	9.03	" -88	18.90*	" -76	24.74**
	4	" -72	3.27	" -76	16.06*	" -93	4.45	" -80	9.99
	4	" -74	38.32**	" -78	5.78	" -95	11.41	" -83	2.50
	4	" -77	7.20	" -80	3.11	" -98	3.94	" -96	1.05
Parents & bulks	4		11.72		14.86		8.31		11.78
Error (b)	128		5.07		6.43		6.70		5.65

* Significant at the 5% level. ** Significant at the 1% level.

but cross No. 3715 in 1945. This cross had the lowest F value of the four crosses for its mean square of F_3 family progenies in 1946. The average yield differences among the F_4 lines within F_3 families were highly significant for each cross in this test. Only a few of the individual mean squares for F_4 lines within F_3 families, however, were significant when tested against the pooled subplot error mean square.

The analyses of the 1946 yield data indicated a tendency for the means of the F_3 family progenies to regress toward the cross means. Part of this tendency was no doubt due to the small plot size and number of replications in the F_3 line test in 1945, which probably resulted in some inaccuracies in the yield evaluations of those lines. Furthermore, five F_4 lines constituted a very small sample of the total possible number of lines that could have been selected to represent the progeny of each F_3 family. It also would have been preferable to have had larger plots and more replications in the 1946 test. It was practically impossible, however, to correct these shortcomings because of the definite limitations on seed from individual plants. Consequently, it would have been difficult to improve on the reliability of the conclusions drawn on the basis of these data.

Maturity

The mean dates of maturity of the F_4 lines, parents, and bulk generations in each cross in 1946, as compared to the maturities of the parental F_2 plants and F_3 lines in 1944 and 1945, respectively, are found in Tables 29 to 32. In contrast to the yield data, the range in mean maturity of the F_3 family progenies was greater for each cross in 1946 than the range in maturity of the parental F_3 lines in 1945. Inasmuch as the extremely early and late F_3 lines were eliminated before sampling the 1945 yield distributions for lines to continue the study, this result was somewhat unexpected. The growing season in 1945 was too cool for rapid growth and caused the maturity dates to be somewhat closer than usual. The 1946 season, on the other hand, was more favorable for normal growth and maturation. The type of season, therefore, probably influenced the results. The dates of maturity of the bulk generations in each cross in the 1946 test reflected average differences among the crosses similar to those previously observed.

As shown by the analyses of variance in Table 33, the differences in maturity among the F_3 family progenies were highly significant in each cross. The great majority of the differences among F_4 lines within each of the F_3 families also were highly significant. This would indicate that there was still considerable segregation for factors conditioning maturity among the F_3 lines which were progeny-tested in the F_4 generation.

Height

The mean plant heights for the 1946 test of F_4 lines, parents,

Table 29. Maturities of F_2 plants in 1944 and the mean maturities of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 1415 (Mukden x Richland), together with the maturities of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Maturity date)	F_3 line (Maturity date)	F_4 lines (Maturity dates) 1	2	3	4	5	Mean
1415-22	9-29	10-2	9-17	9-23	9-19	9-16	9-20	9-19
1415-25	9-25	10-2	9-21	9-20	9-23	9-19	9-19	9-20
1415-29	9-25	10-3	9-19	9-20	9-19	9-19	9-20	9-19
1415-30	9-26	10-1	9-24	9-26	9-26	9-15	9-17	9-22
1415-32	9-29	10-3	9-23	9-21	9-20	9-29	9-23	9-23
1415-42	9-28	10-4	9-19	9-14	9-22	9-[illegible]	9-20	9-19
1415-44	10-6	10-5	9-25	9-22	9-27	9-27	9-24	9-25
1415-50	9-24	10-1	9-19	9-21	9-16	9-18	9-19	9-19
1415-56	9-27	10-2	9-22	9-24	9-20	9-18	9-19	9-20
1415-57	9-17	9-30	9-23	9-14	9-18	9-18	9-17	9-18
1415-60	9-24	10-2	9-20	9-21	9-20	9-15	9-14	9-18
1415-63	9-19	9-30	9-16	9-20	9-18	9-22	9-16	9-18
1415-72	9-22	10-1	9-20	9-16	9-22	9-17	9-22	9-19
1415-74	9-27	10-5	9-15	9-8	9-20	9-25	9-19	9-18
1415-77	9-24	10-3	9-19	9-16	9-18	9-18	9-19	9-18

Mukden	Richland	Bulk F_3	Bulk F_4	Bulk F_5
9-25	9-17	9-23	9-24	9-22

Mean maturity of all entries in 1946 test
9-20

Table 30. Maturities of F_2 plants in 1944 and the mean maturities of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 2715 (Manchuria 13-177 x Richland), together with the maturities of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Maturity date)	F_3 line (Maturity date)	F_4 lines (Maturity dates)					
			1	2	3	4	5	Mean
2715- 4	9-16	10-2	9-25	9-27	9-8	9-23	10-2	9-23
2715-17	9-17	9-27	9-18	9-12	9-15	9-19	9-25	9-18
2715-23	10-2	10-12	9-21	9-27	10-9	10-5	9-27	9-30
2715-30	9-20	10-4	9-25	9-24	9-30	9-29	9-28	9-27
2715-31	9-16	10-1	9-20	9-18	9-17	9-19	9-19	9-19
2715-38	10-2	10-12	10-3	10-9	9-29	9-25	10-9	10-3
2715-40	9-21	9-30	9-19	9-13	9-24	9-23	9-21	9-20
2715-51	10-5	10-11	10-12	9-27	9-27	10-2	10-1	10-2
2715-56	9-27	10-2	9-15	9-21	9-16	9-24	9-18	9-19
2715-58	10-12	10-12	10-14	10-8	9-26	10-3	10-20	10-8
2715-63	10-8	10-12	9-30	10-7	10-8	9-29	10-2	10-3
2715-72	10-6	10-9	9-21	10-1	10-7	10-6	10-9	10-3
2715-76	9-30	10-10	9-24	10-7	9-13	9-23	10-10	9-27
2715-78	9-15	10-3	9-25	9-29	9-20	9-12	9-21	9-21
2715-80	9-23	10-11	10-1	10-7	10-1	10-7	10-3	10-4

Manchuria 13-177	Richland	Bulk F_3	Bulk F_4	Bulk F_5
10-6	9-18	10-7	10-9	10-8

Mean maturities of all entries in 1946 test
9-27

Table 31. Maturities of F_2 plants in 1944 and the mean maturities of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3515 (P.I. 79885 x Richland), together with the maturities of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Maturity date)	F_3 line (Maturity date)	F_4 lines (Maturity dates) 1	2	3	4	5	Mean
3515- 3	9-16	9-30	9-14	9-16	9-12	9-15	9-14	9-14
3515-16	9-18	10-3	9-23	9-21	9-25	9-17	9-21	9-21
3515-18	9-26	10-8	9-24	9-25	9-23	9-25	9-22	9-24
3515-29	9-22	10-1	9-19	9-20	9-27	9-13	9-20	9-20
3515-37	9-16	9-27	9-14	9-16	9-19	9-13	9-9	9-14
3515-44	9-17	9-29	9-16	9-19	9-13	9-11	9-23	9-17
3515-51	9-17	10-2	9-23	9-15	9-20	9-28	9-15	9-20
3515-67	9-17	10-3	9-22	9-22	9-17	9-21	9-20	9-20
3515-68	9-26	10-8	9-23	10-2	9-27	9-22	9-29	9-27
3515-73	9-27	10-7	9-18	9-28	9-24	9-20	9-30	9-24
3515-82	9-16	9-30	9-20	9-24	9-18	9-15	9-17	9-19
3515-88	9-23	10-4	9-18	9-27	9-26	9-21	9-13	9-21
3515-93	10-1	10-8	9-26	9-22	9-21	9-30	9-26	9-25
3515-95	9-17	10-4	9-22	9-26	9-38	9-20	9-18	9-23
3515-98	9-15	10-1	9-18	9-15	9-23	9-14	9-12	9-16

P.I. 79885	Richland	Bulk F_3	Bulk F_4	Bulk F_5
9-16	9-16	9-21	9-25	9-24

Mean maturity of all entries in 1946 test
9-20

Table 32. Maturities of F_2 plants in 1944 and the mean maturities of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3715 (P.I. 89009-2 x Richland), together with the maturities of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Maturity date)	F_3 line (Maturity date)	F_4 lines (Maturity date) 1	2	3	4	5	Mean
3715-15	9-29	10-8	9-29	9-30	9-27	10-2	9-28	9-29
3715-18	9-29	10-11	9-27	9-28	10-4	10-4	10-5	10-2
3715-20	9-28	10-7	10-2	9-29	9-25	9-30	10-3	9-30
3715-23	9-26	10-6	9-19	9-18	9-20	9-19	9-22	9-20
3715-25	9-30	10-11	9-28	10-4	9-13	9-29	10-5	9-28
3715-26	9-27	10-9	9-30	9-30	10-2	9-27	9-17	9-27
3715-39	10-10	10-11	9-25	9-27	9-28	10-6	9-30	9-29
3715-48	9-17	10-3	9-21	9-19	9-25	9-27	9-23	9-23
3715-53	9-27	10-9	10-10	10-7	10-7	10-2	10-8	10-7
3715-68	9-30	10-12	9-17	10-7	10-1	10-3	10-5	10-1
3715-73	10-2	10-10	9-13	10-1	10-3	10-7	9-26	9-28
3715-76	9-27	10-10	9-15	10-6	9-14	9-11	9-10	9-18
3715-80	9-30	10-11	9-29	9-28	10-3	9-25	9-16	9-26
3715-83	9-30	10-11	9-30	9-15	9-30	10-4	10-6	9-29
3715-96	10-7	10-10	9-28	9-28	10-1	9-30	9-30	9-29

P.I. 89009-2	Richland	Bulk F_3	Bulk F_4	Bulk F_5
9-28	9-16	10-4	10-5	10-5

Mean maturity of all entries in 1946 test
9-28

Table 33. Analyses of variance of maturities obtained in 1946 test of F_4 lines, parents, and bulk populations in each of four soybean crosses.

Source of variation	D.F.	Cross and F_2 plant number (Mukden x Richland)	Mean square	Cross and F_2 plant number (Manchuria 13-177 x Richland)	Mean square	Cross and F_2 plant number (P.I. 79885 x Richland)	Mean square	Cross and F_2 plant number (P.I. 89009-2 x Richland)	Mean square
Whole Plot:									
Replications	2		85.72		45.73		351.91		92.27
F_3 family progenies	15		72.31**		671.60**		204.59**		317.76**
Error (a)	30		7.73		10.33		9.34		3.96
Subplot:									
F_4 lines within F_3 families	64		29.44**		129.96**		48.81**		115.64**
	4	1415-22	20.33**	2715-4	255.33**	3515-3	6.43*	3715-15	9.23**
	4	" -25	6.33**	" -17	69.73**	" -16	26.27**	" -18	39.57**
	4	" -29	.83	" -23	150.50**	" -18	6.43*	" -20	34.43**
	4	" -30	80.90**	" -30	16.73**	" -29	74.40**	" -23	5.43**
	4	" -32	40.07**	" -31	3.57	" -37	38.00**	" -25	240.57**
	4	" -42	27.57**	" -38	120.40**	" -44	69.10**	" -26	112.43**
	4	" -44	10.33**	" -40	63.83**	" -51	92.57**	" -39	48.23**
	4	" -50	7.73**	" -51	110.77**	" -67	11.07**	" -48	29.23**
	4	" -56	16.77**	" -56	42.17**	" -68	55.57**	" -53	27.23**
	4	" -57	30.23**	" -58	267.43**	" -73	78.00**	" -68	178.83**
	4	" -60	31.60**	" -63	52.40**	" -82	37.73**	" -73	249.23**
	4	" -63	21.07**	" -72	155.43**	" -88	96.67**	" -76	344.10**
	4	" -72	24.23**	" -76	384.57**	" -93	41.17**	" -80	127.00**
	4	" -74	118.90**	" -78	118.10**	" -95	54.77**	" -83	196.23**
	4	" -77	3.83*	" -80	28.90**	" -98	53.60**	" -96	4.57*
Parents & bulks			30.23**		239.43**		39.17**		203.90**
Error (b)	128		1.57		1.79		2.26		1.46

* Significant at the 5% level. ** Significant at the 1% level.

and bulk generations in each cross appear in Tables 34 to 37. The heights of the parental F_2 plants and F_3 lines in 1944 and 1945, respectively, also are included. These results showed that the differences in height among the F_4 lines in each F_3 family of the four crosses were very similar to the differences in maturity among the same lines. In a few of the F_3 families their progenies in the F_4 generation were reasonably uniform for plant height. Most of them, however, were quite variable, as indicated by their breeding behavior for height. In addition, the average heights of the F_3 family progenies in 1946 exhibited height ranges of about the same extent as the parental F_3 lines in 1945.

The mean heights of the bulk populations in each cross in this test were consistent with previous observations. The bulk generations of cross No. 3715 again were definitely above Richland, the taller parent, in height. The bulk populations of the other crosses were intermediate to the parents in height except in cross No. 2715, where they equaled the taller parent. The mean heights of all entries in each of the four crosses indicated that cross Nos. 1415 and 2715 contained the greatest number of tall F_4 lines. Cross No. 3515, on the other hand, contained the most short F_4 lines. These means were comparable because the F_3 families included in the test were unselected for plant height.

Table 38 gives the analyses of variance of plant heights in the 1946 test. The F_3 family progenies differed significantly in

Table 34. Heights of F_2 plants in 1944 and the mean heights of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 1415 (Mukden x Richland), together with the heights of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Height in inches)	F_3 line (Height in inches)	F_4 lines (Heights in inches) 1	2	3	4	5	Mean
1415-22	34	38	35	40	39	36	40	38
1415-25	36	40	40	40	41	38	40	40
1415-29	32	37	35	38	38	36	39	37
1415-30	40	41	44	40	37	36	35	38
1415-32	31	39	38	36	40	41	36	38
1415-42	34	33	37	30	33	34	37	34
1415-44	39	38	41	36	37	38	40	38
1415-50	35	40	40	39	35	36	36	37
1415-56	35	39	41	38	40	42	37	40
1415-57	32	35	36	33	35	35	38	35
1415-60	36	41	41	41	41	39	36	40
1415-63	28	36	37	35	37	37	34	36
1415-72	35	37	34	32	39	37	38	36
1415-74	38	38	36	27	37	33	41	35
1415-77	30	33	32	29	31	32	32	31

Mukden	Richland	Bulk F_3	Bulk F_4	Bulk F_5
41	33	38	37	39

Mean height of all entries in 1946 test
37

Table 35. Heights of F_2 plants in 1944 and the mean heights of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 2715 (Manchuria 13-177 x Richland), together with the heights of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Height in inches)	F_3 line (Height in inches)	F_4 lines (Heights in inches)					
			1	2	3	4	5	Mean
2715- 4	29	34	35	36	28	34	35	34
2715-17	33	33	33	31	31	33	37	33
2715-23	42	39	37	37	41	39	40	39
2715-30	37	37	35	37	35	37	36	36
2715-31	35	35	37	36	37	37	37	37
2715-38	36	38	36	44	35	36	38	38
2715-40	32	34	34	30	35	39	34	34
2715-51	38	38	40	35	36	38	40	38
2715-56	35	36	32	36	35	35	35	34
2715-58	38	38	39	37	35	37	42	38
2715-63	36	36	40	41	39	39	41	40
2715-72	32	37	32	35	37	37	39	36
2715-76	36	35	36	39	33	35	40	37
2715-78	32	36	36	40	35	33	36	36
2715-80	35	36	40	42	39	43	41	41

Manchuria 13-177	Richland	Bulk F_3	Bulk F_4	Bulk F_5
38	32	38	38	39

Mean height of all entries in 1946 test
37

Table 36. Heights of F_2 plants in 1944 and the mean heights of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3515 (P.I. 79885 x Richland), together with the heights of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Height in inches)	F_3 line (Height in inches)	F_4 lines (Heights in inches)					
			1	2	3	4	5	Mean
3515- 3	17	27	28	29	28	27	26	27
3515-16	16	32	28	30	34	29	31	30
3515-18	27	33	32	32	32	34	33	32
3515-29	23	30	32	30	26	28	26	29
3515-37	16	30	29	26	27	26	26	27
3515-44	26	30	31	31	28	29	32	30
3515-51	25	32	31	30	30	32	29	31
3515-67	18	28	29	29	29	28	28	29
3515-68	32	34	36	24	38	34	38	34
3515-73	18	27	24	27	27	26	28	26
3515-82	27	33	33	32	34	29	34	32
3515-88	24	30	29	37	36	32	26	32
3515-93	29	37	36	34	38	39	37	37
3515-95	14	28	29	36	36	29	30	32
3515-98	33	34	33	34	36	33	31	34

P.I. 79885	Richland	Bulk F_3	Bulk F_4	Bulk F_5
28	33	31	32	32

Mean height of all entries in 1946 test
31

Table 37. Heights of F_2 plants in 1944 and the mean heights of their progenies in the F_3 generation in 1945 and of five F_4 generation selections per F_3 line in 1946 for cross No. 3715 (P.I. 89009-2 x Richland), together with the heights of the parents and three bulk generations in 1946.

Cross and F_2 plant number	F_2 plant (Height in inches)	F_3 line (Height in inches)	F_4 lines (Heights in inches)					
			1	2	3	4	5	Mean
3715-15	29	40	40	43	34	36	40	39
3715-18	32	37	37	39	35	29	39	36
3715-20	38	36	32	37	34	36	39	36
3715-23	31	35	33	33	33	35	34	34
3715-25	29	36	35	37	29	34	38	34
3715-26	38	39	41	41	42	39	36	40
3715-39	37	39	38	38	37	34	40	37
3715-48	32	32	32	32	33	34	34	33
3715-53	34	39	40	37	39	36	32	37
3715-68	32	38	27	37	36	22	37	32
3715-73	33	39	29	38	32	38	36	35
3715-76	37	39	30	34	29	31	30	31
3715-80	34	36	35	38	37	34	31	35
3715-83	32	37	34	27	36	31	37	33
3715-96	32	41	37	38	38	38	38	38

P.I. 89009-2	Richland	Bulk F_3	Bulk F_4	Bulk F_5
30	33	36	37	37

Mean height of all entries in 1946 test
35

Table 38. Analyses of variance of plant heights obtained in 1946 test of F_4 lines, parents, and bulk populations in each of four soybean crosses.

Source of variation	D.F.	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square	Cross and F_2 plant number	Mean square
		(Mukden x Richland)		(Manchuria 13-177 x Richland)		(P.I. 79885 x Richland)		(P.I. 89009-2 x Richland)	
Whole Plot:									
Replications	2		146.74		90.52		8.41		32.66
F_3 family progenies	15		79.49**		72.84**		118.52**		92.06**
Error (a)	30		2.36		6.68		1.81		3.46
Subplot:									
F_4 lines within F_3 families	64		19.51**		16.60**		18.33**		32.06**
	4	1415-22	18.23**	2715-4	28.90**	3515-3	4.90**	3715-15	34.90**
	4	" -25	2.93	" -17	18.00**	" -16	13.57**	" -18	47.60**
	4	" -29	9.50**	" -23	11.07**	" -18	2.07	" -20	23.10**
	4	" -30	42.07**	" -30	2.17	" -29	18.27**	" -23	2.40
	4	" -32	18.00**	" -31	1.17	" -37	4.90**	" -25	39.60**
	4	" -42	21.10**	" -38	38.43**	" -44	6.50**	" -26	18.50**
	4	" -44	12.50**	" -40	26.57**	" -51	3.40	" -39	14.43**
	4	" -50	15.10**	" -51	19.43**	" -67	1.33	" -48	2.27
	4	" -56	14.77**	" -56	8.77**	" -68	96.33**	" -53	30.43**
	4	" -57	8.57**	" -68	18.77**	" -73	5.73**	" -68	145.43**
	4	" -60	13.40**	" -63	3.33*	" -82	13.43**	" -73	44.57**
	4	" -63	6.57**	" -72	19.07**	" -88	57.77**	" -76	10.00**
	4	" -72	26.57**	" -76	19.50**	" -93	10.67**	" -80	25.27**
	4	" -74	76.57**	" -78	22.23**	" -95	43.83**	" -83	47.67**
	4	" -77	4.00*	" -80	7.33**	" -98	7.77**	" -96	.67
Parents & bulks	4		22.33**		20.83**		10.77**		26.07**
Error (b)			1.54		1.10		1.40		1.50

* Significant at the 5% level. ** Significant at the 1% level.

height in every instance. The average differences among F_4 lines within F_3 families in each of the crosses also were highly significant. Only a few of the F_3 families contained F_4 lines not significantly different among themselves in plant height. These results, like the comparable ones for maturity, indicated that the majority of the F_3 lines were heterozygous for genes conditioning plant height.

Lodging score

Differences in lodging resistance among the F_4 lines in 1946 were quite large in many of the F_3 families included in this test, as shown by the lodging scores in Tables 39 to 42. The lodging scores of only the parental F_3 lines in 1945 were included for comparison, as no lodging scores were taken on the F_2 plants in 1944. These data conformed to expectations based on previous results. Cross Nos. 1415 and 3515 again contained the most lines with good lodging resistance. Cross No. 2715, on the other hand, contained the most lines with a high degree of lodging susceptibility. The mean lodging scores of the bulk generations also indicated similar differences in lodging resistance among the crosses. Each of the crosses, nevertheless, contained F_4 lines worthy of selection for lodging resistance.

Analyses of variance of the lodging scores of the F_4 lines, parents, and bulk generations in 1946 showed that the F_3 family progenies in each of the crosses differed significantly for this character. These analyses, which are given in Table 43, also indicated

Table 39. Mean lodging scores of F_4 lines, parents, and bulk generations in 1946 for cross No. 1415 (Mukden x Richland) in comparison with the mean lodging scores of the parental F_3 lines in 1945.

Cross and F_2 plant number	F_3 line (Lodging score)	F_4 lines (Lodging scores) 1	2	3	4	5	Mean
1415-22	2.3	1.3	2.0	2.0	1.0	1.7	1.6
1415-25	2.7	3.3	2.0	3.0	2.7	3.0	2.8
1415-29	2.7	2.3	2.0	2.7	2.0	2.3	2.3
1415-30	2.0	2.0	2.3	2.7	1.7	2.0	2.1
1415-32	2.3	1.7	1.0	2.0	2.7	1.3	1.7
1415-42	2.3	1.3	1.0	1.7	1.3	1.7	1.4
1415-44	2.7	2.3	1.7	3.3	3.3	2.3	2.6
1415-50	2.3	2.0	2.3	2.3	2.0	2.3	2.2
1415-56	2.3	2.0	2.7	2.3	1.7	2.7	2.3
1415-57	1.7	2.3	1.0	1.3	2.3	1.0	1.6
1415-60	2.3	2.0	2.0	2.7	1.7	1.3	1.9
1415-63	2.3	1.7	3.0	2.0	2.7	1.3	2.1
1415-72	1.7	2.0	2.0	2.0	1.7	2.0	1.9
1415-74	2.0	2.0	1.0	2.3	2.7	2.3	2.1
1415-77	1.3	1.3	1.0	1.0	1.0	1.0	1.1

Mukden	Richland	Bulk F_3	Bulk F_4	Bulk F_5
2.7	1.3	2.3	2.7	2.0

Mean lodging score of all entries in 1946 test
2.0

Table 40. Mean lodging scores of F_4 lines, parents, and bulk generations in 1946 for cross No. 2715 (Manchuria 13-177 x Richland) in comparison with the mean lodging scores of the parental F_3 lines in 1945.

Cross and F_2 plant number	F_3 line (Lodging score)	F_4 lines (Lodging scores) 1	2	3	4	5	Mean
2715- 4	2.3	3.0	3.0	1.3	2.0	3.3	2.5
2715-17	2.7	1.3	1.0	1.0	1.3	2.3	1.4
2715-23	2.7	1.0	3.0	3.0	3.0	3.0	2.6
2715-30	2.3	2.3	1.7	3.0	3.0	2.3	2.5
2715-31	3.0	3.0	3.0	2.7	2.7	3.0	2.9
2715-38	3.0	3.3	3.3	3.3	3.0	3.3	3.3
2715-40	2.3	1.7	1.3	2.7	2.0	2.0	1.9
2715-51	3.0	3.0	2.3	2.7	3.0	3.3	2.9
2715-56	3.0	1.3	2.0	1.7	2.7	2.0	1.9
2715-58	2.7	3.7	3.7	2.7	3.0	2.3	3.1
2715-63	3.0	3.0	3.0	3.0	3.0	3.0	3.0
2715-72	2.0	1.7	2.0	3.0	2.3	3.0	2.4
2715-76	3.3	3.0	3.3	1.7	3.0	4.0	3.0
2715-78	2.7	2.7	3.0	2.7	1.7	3.0	2.6
2715-80	2.7	3.3	3.0	3.3	3.3	3.0	3.2

Manchuria 13-177	Richland	Bulk F_3	Bulk F_4	Bulk F_5
4.0	1.3	3.0	3.7	3.3

Mean lodging score of all entries in 1946 test
2.6

Table 41. Mean lodging scores of F_4 lines, parents, and bulk generations in 1946 for cross No. 3515 (P.I. 79885 x Richland) in comparison with the mean lodging scores of the parental F_3 lines in 1945.

Cross and F_2 plant number	F_3 line (Lodging score)	F_4 lines (Lodging scores)					
		1	2	3	4	5	Mean
3515- 3	1.7	1.3	1.3	1.0	1.3	1.0	1.2
3515-16	2.7	1.3	2.3	2.3	1.3	2.7	2.0
3515-18	2.3	3.0	2.7	2.3	3.0	2.3	2.7
3515-29	3.0	1.0	1.7	2.7	1.3	1.0	1.5
3515-37	2.0	1.0	1.3	2.7	1.0	1.0	1.4
3515-44	2.0	1.0	1.0	1.0	1.0	2.0	1.2
3515-51	2.3	2.3	2.0	2.3	2.3	2.3	2.3
3515-67	1.7	2.3	2.3	1.3	1.7	2.0	1.9
3515-68	3.7	2.3	1.0	3.0	2.0	3.0	2.3
3515-73	2.3	1.0	2.0	1.7	1.3	2.7	1.7
3515-82	1.3	1.7	2.3	1.7	1.0	1.0	1.5
3515-88	2.7	2.0	3.0	2.7	2.7	1.3	2.3
3515-93	2.7	3.3	2.7	2.0	3.3	3.0	2.9
3515-95	2.0	1.3	2.7	3.0	2.0	1.3	2.1
3515-98	2.3	2.3	2.3	3.0	2.0	1.3	2.2

P.I. 79885	Richland	Bulk F_3	Bulk F_4	Bulk F_5
2.7	1.3	2.0	2.7	2.3

Mean lodging score of all entries in 1946 test
2.0

Table 42. Mean lodging scores of F_4 lines, parents, and bulk generations in 1946 for cross No. 3715 (P.I. 89009-2 x Richland) in comparison with the mean lodging scores of the parental F_3 lines in 1945.

Cross and F_2 plant number	F_3 line (Lodging score)	F_4 lines (Lodging scores) 1	2	3	4	5	Mean
3715-15	1.7	2.0	2.0	1.3	1.3	1.7	1.7
3715-18	2.7	2.7	3.0	3.0	1.3	3.0	2.6
3715-20	2.7	3.0	2.3	2.7	3.7	3.7	3.1
3715-23	2.7	1.3	1.3	2.0	2.0	2.3	1.8
3715-25	3.0	3.0	3.0	1.0	2.7	3.7	2.7
3715-26	3.3	3.0	3.0	3.7	2.7	1.3	2.7
3715-39	2.7	3.0	3.0	3.3	3.0	3.3	3.1
3715-48	2.3	3.0	2.7	3.3	4.0	3.3	3.3
3715-63	2.0	1.3	2.3	2.0	1.0	1.0	1.5
3715-68	2.3	1.0	2.3	2.3	1.0	2.7	1.9
3715-73	2.7	1.0	2.7	1.7	2.7	1.7	1.9
3715-76	2.7	1.0	2.7	1.0	1.0	1.0	1.3
3715-80	2.7	3.0	2.3	3.0	1.7	1.3	2.3
3715-83	2.0	1.3	1.0	1.3	1.0	2.7	1.5
3715-96	2.7	1.7	1.7	2.7	2.3	1.3	1.9

P.I. 89009-2	Richland	Bulk F_3	Bulk F_4	Bulk F_5
2.0	1.0	3.0	3.3	3.0

Mean lodging score of all entries in 1946 test
2.2

Table 43. Analyses of variance of lodging scores obtained in 1946 test of F_4 lines, parents, and bulk populations in each of four soybean crosses.

Source of variation	D.F.	Cross and F_2 plant number (Mukden x Richland)	Mean square	Cross and F_2 plant number (Manchuria 13-177 x Richland)	Mean Square	Cross and F_2 plant number (P.I. 79885 x Richland)	Mean square	Cross and F_2 plant number (P.I. 89009-2 x Richland)	Mean square
Whole Plot:									
Replications	2		7.33		.99		8.79		4.41
F_3 family progenies	15		2.89**		4.07**		3.66**		5.91**
Error (a)	30		.51		.60		.62		.38
Subplot:									
F_4 lines within F_3 families	64		.72**		1.06**		1.01**		1.42**
	4	1415-22	.57*	2715-4	2.10**	3515-3	.10	3715-15	.33
	4	" -25	.77*	" -17	.90**	" -16	1.17**	" -18	1.57**
	4	" -29	.23	" -23	2.40**	" -18	.33	" -20	1.07**
	4	" -30	.43	" -30	.93**	" -29	1.43**	" -23	.60**
	4	" -32	1.23**	" -31	.10	" -37	1.57**	" -25	3.00**
	4	" -42	.23	" -38	.07	" -44	.60**	" -35	2.23**
	4	" -44	1.57**	" -40	.73**	" -51	.07	" -39	.10
	4	" -50	.10	" -51	.43	" -67	.57*	" -48	.73**
	4	" -56	.57*	" -56	.73**	" -68	2.07**	" -53	1.10**
	4	" -57	1.40**	" -58	1.07**	" -73	1.23**	" -68	1.93**
	4	" -60	.73*	" -63	.00	" -82	.93**	" -73	1.57**
	4	" -63	1.43**	" -72	1.07**	" -88	1.33**	" -76	1.67**
	4	" -72	.07	" -76	2.17**	" -93	.93**	" -80	1.73**
	4	" -74	1.23**	" -78	.90**	" -95	1.73**	" -83	1.43**
	4	" -77	.07	" -80	.10	" -98	1.10**	" -96	.90**
Parents & bulks	4		.93**		3.23**		.93**		2.77**
Error (b)	128		.23		.18		.17		.15

* Significant at the 5% level.   ** Significant at the 1% level.

that most of these F_3 families in each cross consisted of F_4 lines significantly different among themselves for lodging resistance. Many of the parental F_3 lines, therefore, were heterozygous for factors affecting the amount of lodging.

Correlations

Each group of five sister F_4 lines in the 1946 test descended from a single F_2 plant in 1944 and its progeny in the F_3 generation in 1945. In the previous section all correlations for maturity and height between F_2 plants and their progenies in the F_3 generation were highly significant. Similar correlations for yield were considered too small to be of value for selecting superior F_2 plants. The correlations between the F_2 and F_4 generations and between the F_3 and F_4 generations for these agronomic characters, as recorded in Table 44, showed the same general tendencies. Only two of the correlations for yield were significant. One of these, that between F_2 plants and the means of their F_4 lines in cross No. 3515, was significantly negative and thus quite contrary to expectation. The other significant correlation for yield was between F_3 plants and their F_4 lines in cross No. 1415. Individual F_3 plant data for this cross made it possible to calculate this correlation.

The most important group of yield correlations was that between the F_3 lines and their progeny F_4 lines. Three of these were very close to zero, thereby indicating almost a complete lack of

Table 44. Correlation coefficients between generations grown in successive years for yields, maturities, heights, and lodging scores of segregates in each of four soybean crosses.

Character and variates correlated	D.F.	Mukden x Richland (Cross No. 1415)	Manchuria 13-177 x Richland (Cross No. 2715)	P.I. 79885 x Richland (Cross No. 3515)	P.I. 89009-2 x Richland (Cross No. 3715)
Seed yield:					
F_2 plant and mean of F_4 lines	13	.2602	.3465	-.6511**	-.0079
F_3 plant and F_4 line	73	.3026**			
F_3 line and mean of F_4 lines	13	.4602	.0442	-.0338	.0836
Maturity:					
F_2 plant and mean of F_4 lines	13	.7355**	.8078**	.7887**	.3240
F_3 plant and F_4 line	73	.7396**			
F_3 line and mean of F_4 lines	13	.3529	.9243**	.9240**	.3684
Height:					
F_2 plant and mean of F_4 lines	13	.4218	.6077*	.7179**	.1429
F_3 plant and F_4 line	73	.8470**			
F_3 line and mean of F_4 lines	13	.8514**	.6094*	.8419**	.4862
Lodging score:					
F_3 line and mean of F_4 lines	13	.7131**	.3866	.4596	.4392

* Significant at the 5% level. ** Significant at the 1% level.

association for yield between these generations. If this lack of relationship were true for soybean crosses in general, selection for yield on the basis of pedigree yield tests in the F_3 generation would certainly be of doubtful value in the breeding program.

A number of the correlations for maturity and height in Table 44 were statistically significant. All of them were positive. Maturity and height measurements on F_2 plants and their replicated progeny rows in the F_3 generation, therefore, were of value in predicting results in the succeeding generation of these soybean crosses. Only one of the crosses showed a significant correlation for lodging score between the F_3 and F_4 generations. Consequently, selection for lodging resistance on the basis of F_3 data would have been less effective than selection for differences in maturity and height.

Character Relationships

The main objective of most soybean breeding programs is the development of adapted, high yielding, lodging resistant varieties, tall enough to harvest with a combine. The extent of relationships between maturity, height, lodging resistance, and yield in segregating populations of soybean crosses may definitely influence the realization of this objective.

In the pedigree phase of this study correlations were used to measure the degree of association between agronomic characters in the F_2, F_3, and F_4 generations of each cross. As shown in Table 45,

Table 45. Simple and partial correlation coefficients between agronomic characters of one hundred F_2 plants, seventy-seven F_3 lines, and seventy-five F_4 lines in each of four soybean crosses.

Characters correlated	Mukden x Richland (Cross No. 1415)			Manchuria 13-177 x Richland (Cross No. 2715)			P.I. 79885 x Richland (Cross No. 3515)			P.I. 89009-2 x Richland (Cross No. 3715)		
	F_2 1944	F_3 1945	F_4 1946	F_2 1944	F_3 1945	F_4 1946	F_2 1944	F_3 1945	F_4 1946	F_2 1944	F_3 1945	F_4 1946
Maturity (m) and height (h)												
r_{mh}	.7393	.5728	.5141	.7611	.7914	.7823	.6072	.3757	.4412	.5581	.5147	.5045
$r_{mh.y}$	.6730	.5381	.4824	.6342	.7964	.7855	.4225	.4034	.4502	.3967	.5059	.5409
Maturity (m) and yield (y)												
r_{my}	.4910	.3918	.2278	.5607	.0430	.0039	.5763	.5406	-.0974	.4782	.1325	.4977
$r_{my.h}$	.2904	.3241	.1057	.1575	-.1526	-.1150	.3617	.3719	-.1393	.2367	.0737	.5349
Height (h) and yield (y)												
r_{hy}	.4247	.2329	.2735	.6301	.1706	.0961	.5555	-.0106	.0620	.5669	.1359	.0735
$r_{hy.m}$	.1052	.1127	.1873	.3788	.2235	.1493	.3166	-.1591	.1176	.4117	.0797	-.2371
Lodging score (l) and yield (y)												
r_{ly}		.2078	.3590		.0873	.1262		.2537	.1257		.1602	.0947

Correlation coefficients at the 5% and 1% level of significance

	F_2	F_3	F_4
5%	.197	.225	.228
1%	.257	.293	.296

all correlations between maturity and height were positive and highly significant in every generation of each cross, irrespective of differences in yield. All simple correlations between maturity and yield and height and yield of F_2 plants also were positive and highly significant. The partial correlations for the same characters were, in most instances, considerably lower. In other words, the degree of relationship between maturity and yield and height and yield of the F_2 plants was definitely less when height and maturity, respectively, were held constant. The simple correlations between the same characters in the F_3 and F_4 generations were even smaller. Three of the eight simple correlations between maturity and yield in these generations were positive and highly significant. Two of the eight between height and yield were significantly positive. All others were non-significant. In the majority of cases the partial correlations for the same characters were smaller than the corresponding simple correlations. The correlations between lodging and yield all were positive but only one was highly significant and another significant. The results indicated that the most consistent association occurred between maturity and height.

The nature of these relationships has a bearing on the attainment of soybean breeding objectives. The strong positive association between maturity and height emphasized the difficulty of securing desired tall early segregates in these populations. As the taller plants and lines tended to yield more, selection for tallness favored selection for yield. Early maturity, on the other hand, was not associated with high yield. There also was a tendency for the most lodging resistant lines to yield less. Character relationships, therefore, were factors which affected selection potentialities to varying degrees in the segregating populations of the crosses included in this study.

DISCUSSION

Hybridization followed by selection in the segregating populations is the most promising method of obtaining new and improved varieties of soybeans. Several outstanding varieties have been developed by the use of this breeding procedure and many promising selections from crosses are now in the early stages of testing in regional trials. Despite this evidence of success, however, there are disturbing features about the use of hybridization in soybean improvement that are in need of clarification. A large number of crosses between varieties and strains of this crop have failed to produce desirable recombinations in the resulting segregates. Although many of these crosses apparently have shown transgressive segregation in the F_2 and F_3 generations for factors conditioning various important characters, only a very few have given any promising new types after subsequent selection. Such results have led to considerable confusion among different soybean breeders.

Several possible reasons can be postulated for this apparent failure to obtain or detect improved segregates in many soybean crosses. First of all, as soybean breeding is a comparatively recent development, there has been little opportunity to evaluate varieties as parental material in crosses. Consequently, many crosses have been made which probably would not have been made had such information been available. Moreover, a number of these crosses were made between related types, and as a result, the potentialities for new recombinations were decreased. Another possible reason lies in the methods used to evaluate crosses in the generations following hybridization. Soybean breeders, in general, have utilized the same procedures for handling segregating populations of crosses as those employed by breeders of the self-pollinated cereals. Soybean varieties, however, are considerably more responsive to environmental fluctuations, especially changes in photoperiod, than small grain varieties. In addition, soybeans are a full-season crop and hence, response to variations in climate include a greater time factor than in small grains. Consequently, soybean strains frequently react differentially in two localities even though soil, temperature, and rainfall conditions may be very similar. Selection for differences among segregates in one locality or year, therefore, may not insure similar performance in another locality or year, depending upon seasonal fluctuations in environment. It is conceivable, therefore, that segregating populations of soybean crosses may not be as well adapted as is commonly supposed to breeding methods used in cereals. This might pertain especially to the methods used for early generation testing in small grain crosses.

Immer (14) attempted to relate the average yield performance of spaced F_1 plants in several barley crosses with that of their bulk populations in drilled plots in subsequent generations. Considerable lack of agreement was found between the F_1 and the subsequent generation. A similar lack of agreement between the extent of heterosis for seed yields in the F_1 and succeeding generations was found by Weiss, Weber, and Kalton (32) in a number of soybean crosses. Both reports stressed the impracticability of making such F_1 yield studies, primarily because of the limited supplies of crossed seed. The conclusions from F_1 generation results reported herein agreed very well with previous investigations. Mukden x Richland, the cross which showed the least superiority over the common parent in the F_1 generation spaced plant tests, was the highest yielding of the four crosses in replicated trials of the bulk F_2 to F_4 populations. Two other crosses were considerably above the common parent in seed yield in the F_1 generation but no better than it in the bulk tests of the succeeding generations. A similar lack of association was noted between the F_1 yields and the mean yields of seventy-seven randomly selected F_3 lines in each cross. Little or no information about the yielding potentialities of the four crosses was gained, therefore, by measuring seed yields on spaced F_1 plants.

In addition to seed yield, height and maturity differences among the four crosses were evaluated in the F_1 generation in comparison to Richland. Although based only on a few F_1 plants per cross, these comparisons were of considerable interest when examined in light of the advanced generation performance of the crosses for the same characters. In the F_1 generation Manchuria 13-177 x Richland and P.I. 89009-2 x Richland were the latest of the crosses, as compared to the maturity of Richland. P.I. 79885 x Richland, on the other hand, was the earliest of the crosses in the same respect. These average maturity differences among the crosses remained quite consistent in all subsequent generations. The average height differences among the crosses in the F_1 generation, as compared to Richland, also persisted in later generations. Only one of the crosses, namely, P.I. 89009-2 x Richland, exceeded both parents in average plant height in the F_1 generation. Moreover, this average height superiority was retained in both bulk and pedigree tests of the F_2 to F_4 generations. Evidently this cross resulted in a combination of complementary genes for plant height. The F_1 generation results for plant height and date of maturity, therefore, were indicative of average differences among the crosses for these characters in advanced generations.

One of the principal disadvantages of bulk population trials of soybean crosses is failure to obtain information on the extent of segregation for factors conditioning height, maturity, lodging resistance, and seed yield because such tests give only average performance records. As an example, Manchuria 13-177 x Richland was one of the latest and tallest of the crosses in the bulk population trials, yet it produced a number of short and early F_2 plants and F_3 lines. Similar contrasts were apparent in the other crosses. Consequently, although the bulk populations of all crosses performed quite consistently for mean maturity, height, and lodging resistance at successive generations in consecutive years, the results were of little value in determining the range of selection potentialities for these characters in each of the crosses. This was especially evident for such a character as early maturity. On the other hand, the average differences among the bulk populations of the crosses did provide some information on intercross selection opportunities for increased height and lodging resistance.

Harlan, Martini, and Stevens (6) and Harrington (9) successfully used early generation tests of bulk populations of barley and wheat crosses, respectively, to detect potentially low yielding crosses. A similar study of the early generation yield performance of seventeen soybean crosses, reported by Weiss, Weber, and Kalton (32), was of little value for predicting the yielding ability of selected segregates. In the same investigation considerable disagreement was found between bulk population yields in different generations, whether grown the same year or in different years. As a result, the inconsistencies observed herein in the bulk population yields of twenty-five soybean crosses at successive generations were not entirely unexpected. The yield differences among the bulk populations of the crosses in the F_2 generation were not very well substantiated by similar tests of the F_3 and F_4 generations in succeeding years. A considerable proportion of these erratic yield results with the bulk populations probably was due to differences in competitive ability both among and within crosses as a consequence of differential segregation for factors conditioning maturity, height, lodging resistance, and possibly even yield. The selective action of early and late fall frosts also may affect the bulk populations of different crosses in a diverse manner. In contrast, bulk populations of small grain crosses usually do not exhibit such extreme variability for the same characters, nor does frost damage become a factor during the reproductive stages. It seems probable, therefore, that early generation testing of bulk populations of crosses in soybeans will not be as practical from a breeding standpoint as similar tests of small grain crosses.

One of the more controversial questions confronting soybean breeders is whether or not to space-plant segregating populations of crosses to facilitate plant selection. This problem is of greatest significance during the F_2 and F_3 generations when opportunities for selection are greatest. Close planting (1 to 3 inch spacing of plants in the row) generally puts the earlier and shorter F_2 and F_3 plants at a serious competitive disadvantage and tends to favor the taller and later segregates. A wider spacing (6 to 12 inch spacing of plants in the row) helps overcome these disadvantages. At the same time, however, space-planting greatly increases the amount of soil heterogeneity and also causes the individual plants to branch more and grow shorter than usual. Consequently, either wide or narrow spacings of plants within the row may interfere with the expression of genetic differences among F_2 and F_3 plants of a cross.

An attempt was made in the pedigree phase of this investigation to determine the value of selection for differences in agronomic characters among spaced F_2 and F_3 plants of four soybean crosses. Non-replicated plantings were used so that conditions would conform to general practice. Seed yield, maturity, and plant height varied considerably not only among the F_2 plants of each cross but also among the plants of several pure breeding parental varieties. As would be expected, because of genetic segregation, the extent of variation among the F_2 plants for each character generally was greater for the crosses than for the varieties. The crosses, however, differed quite markedly in this respect. A better measure of the agronomic differences among the F_2 plants in each cross was obtained by growing a replicated test of their progenies in the F_3 generation. In all but one case the mean agronomic differences among the F_3 lines in each cross were highly significant when analyzed statistically. Moreover, the differences in maturity and plant height among the F_3 lines were strongly associated with parental F_2 plant differences in the previous year. There was, however, little indication of a significant regression of mean seed yields of F_3 lines on parental F_2 plant yields. Similar results were obtained for one of the crosses when agronomic measurements of spaced F_3 plants were correlated with their F_4 line means.

The yield distributions of the F_3 lines in each cross were sampled to continue the study in the F_4 generation. Each F_3 line thus selected was represented in the F_4 generation by the replicated progenies of five of its constituent F_3 plants. The results of this F_4 line test indicated that little homozygosity existed in the F_3

generation for factors conditioning maturity, plant height, and lodging resistance. In most cases there were highly significant differences among F_4 lines within F_3 families for each of these characters. The F_3 family progeny means in each cross also differed significantly for the same characters. Furthermore, the F_4 generation results for maturity, height, and lodging resistance were reasonably associated with the previous performance of the respective parental F_2 plants and F_3 lines. On the basis of this observed breeding behavior, selection for differences in plant height and maturity among spaced F_2 plants and their space planted F_3 progeny rows appears justified as a breeding procedure.

The mean seed yields of F_3 family progenies in the F_4 generation apparently regressed toward the cross means, as only one of the crosses showed significant differences among the means of the F_3 family progenies. The yields of neither the parental F_2 plants nor the parental F_3 lines were associated in a significantly positive manner with the mean yields of their F_3 family progenies in the F_4 line test. Mean yield differences among F_3 lines, therefore, were not substantiated by the results in the succeeding generation. Weiss, Weber, and Kalton (32) likewise found a lack of desirable association between mean seed yields of pedigree lines in the F_3 and their descendant progenies in the F_4 generation. However, they encountered two widely diverse seasons during their study. All investigations reported herein were conducted during reasonably normal seasons.

Consequently, on the basis of these two similar studies, it would seem that neither the bulk nor the pedigree methods of early generation testing in soybean crosses provide much information, at least before the F_4 generation, on the potential yielding ability of subsequent selections.

SUMMARY AND CONCLUSIONS

1. Bulk F_2, F_3, and F_4 populations of twenty-five soybean crosses were grown in replicated trials in successive years and evaluated for seed yield, date of maturity, plant height, and lodging resistance in comparison with three of the parental varieties.

2. None of the bulk populations outyielded Lincoln, the highest yielding parental variety, in any year. A number of them, however, exceeded the other two parental varieties in yield.

3. The bulk populations of the crosses differed considerably in mean agronomic performance in each generation. Moreover, the differences in mean height, maturity, and lodging resistance among the crosses remained relatively consistent from generation to generation, thereby indicating that one bulk generation test would have sufficed for their evaluation.

4. Yield differences among the twenty-five bulk crosses were not consistent from year to year. Although some crosses were high or low in yield performance in each bulk test, others varied considerably in yield from year to year. Consequently, it would have been difficult to detect and eliminate the poorer yielding bulk crosses on the basis of results from a single test.

5. Yield differences between parental varieties were a poor indication of bulk population yield performance of crosses in the early segregating generations.

6. Two of the highest and two of the lowest yielding crosses were selected on the basis of their yield performance in the bulk population trials for a study of breeding behavior at successive generations by the use of the pedigree method.

7. Two spaced F_1 plant studies showed that the extent of heterosis for seed yield among these four crosses in comparison to Richland, the common parent, was not associated to any appreciable degree with differences in subsequent bulk population or pedigree yield performance.

8. Average plant height and maturity differences among the four crosses in the F_1 generation in relation to the common parent persisted in all advanced generation tests.

9. Mean agronomic performance in the F_1 spaced plant studies and in the bulk population trials was not indicative of differences between crosses in the extent of segregation for factors conditioning maturity, height, lodging resistance, and seed yield.

10. Plant height and maturity measurements made on spaced F_2 plants in each cross provided a relatively good estimate of average progeny performance for the same characters in the F_3 and F_4 generations.

11. Seed yield measurements made on spaced F_2 plants were of little or no value in predicting the yield potentialities of their F_3 and F_4 progenies.

12. Replicated tests of the progenies of seventy-seven randomly selected F_2 plants in each cross indicated a high degree of heterozygosity for factors conditioning each agronomic character studied.

13. The results of replicated progeny tests of five randomly selected F_3 plants in each of fifteen families per cross also showed that there was little homozygosity in the F_3 generation for factors conditioning maturity, height, and lodging resistance.

14. Selection for differences in seed yield among F_3 lines did not seem warranted on the basis of results obtained in the F_4 generation.

15. Breeding behavior for lodging resistance appeared somewhat less consistent than breeding behavior for plant height and maturity among the four crosses.

16. All results appeared to justify the conclusion that soybean varieties differ widely in combining ability for factors determining the agronomic characters studied in this investigation.

17. Neither the bulk nor the pedigree methods of early generation testing for yield, as used herein in the four soybean crosses, were very reliable in estimating their yield potentialities at least before the F_4 generation.

18. A strong and consistent positive association was observed between maturity and plant height in the F_2 to F_4 generations of all crosses in the pedigree study. These data indicated that

selection for a combination of tall early plants would have been difficult.

19. Although maturity and plant height generally were positively associated with yield, the degree of relationship was not sufficiently consistent to indicate that desirable combinations of these characters could not have been found in the segregating populations of the four crosses.

20. The degree of association between lodging resistance and yield in the F_3 and F_4 generations of the pedigree study was too small to be of significance.

21. Several reasons were postulated for the differential reaction of soybean crosses, as compared with small grain crosses, to methods of early generation testing for yield.

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